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Spatial and temporal aspects
of plant species conservation

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by Roman numerals:

- I. Pärtel, M., Kalamees, R., Reier, Ü., Tuvi, E-L., Roosalu, 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. Vellak, A. Tuvi E-L, Reier Ü, Kalamees R, Roosalu E. Zobel M, Pärtel M. (in press) Past and Present Effectiveness of Protected Areas for Conservation of Naturally and Anthropogenically Rare Plant Species. *Conservation Biology*.
- III. Vellak, K., Vellak, A., Ingerpuu, N. (2007) Reasons for moss rarity: study in three neighbouring countries. *Biological Conservation* 135, 360–368.

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Author's principal contributions to the papers:

	I	II	III
Original idea		*	
Study design	*	*	*
Data gathering		*	*
Data processing		*	*
Interpretation	*	*	*
Writing	*	*	*

INTRODUCTION

Biodiversity preservation occurs as the main topic in conservation biology. The loss of biodiversity is increasing with growing speed due to anthropogenic changes in natural ecosystems. The roots of biodiversity conservation starting from its own philosophy, stretch broadly into different fields, integrating with economic and social context, and including research about the biotic and abiotic environment (Meffe et al 2006). Knowledge that biodiversity in its biological, functional, and hierarchical variation has its own value, and has value for people, generates understanding about the importance of biodiversity conservation (Orians & Groom 2006). Preservation of biodiversity forms the basis for evolution and, finally, human existence.

Biological systems ranking from the molecular to the ecosystem level are far too complex to be measured and considered in practical nature conservation (Glowka et al 1994). Simplification is needed so that we can operate on more easily understandable levels of biodiversity. Numerous research papers are based on species level (Rozenzweig 2004; Pärtel et al 2004; Sætersdal et al 2005; Reier et al 2005; Stevens 2006; Turner et al 2006) because the number of species is a relatively good measure of biodiversity. Among all species, rare and threatened species have received special attention both in conservation theory and practice (Norris 2004). Uneven distribution of rare and threatened species on the spatial (Wood 2001) and temporal scale (White et al 2006), however, complicates the tasks of practical conservation. The attention of scientists and conservationists is directed to the understanding the principles of distribution of diversity patterns (Pärtel et al 2004) and its temporal changes (Helm et al 2006). Understanding that some changes of biodiversity are delayed after landscape fragmentation leads to additional complications, such as extinction debt (Carroll et al 2004). Habitat loss and species loss are not synchronized – there exists a time lag after disturbance but before extinctions occur (Tilman et al 1994). These ideas indicate that species protection must be analyzed in the wider spatial and temporal context of landscapes and ecosystems (Rosenvald & Löhmus). A practical solution to maintain both rare species and the total biodiversity is the establishment of systems of protected areas; here, spatial and temporal dynamics of protected areas should be taken into consideration.

Only a good scientific knowledge of biodiversity allows its efficient protection, but this knowledge should be aligned with the expectations of society. Overall agreement on aims and methods of conservation procedures has been established through various documents. The principal paper to monitor biodiversity preservation on a global scale is the Convention on Biological Diversity from 1992 and its practical goals for year 2010 (Groom et al 2006). Supported by this document several other international, regional and national level agreements, strategies, directives, conservation legislation have been worked out (Rohlf 2006). Although these documents include quantitative and qualitative indices to understand how efficiently biodiversity is maintained, the decisions based on these indices still need careful scientific analysis. One fact

emerges clearly: effective nature conservation can not be organized spontaneously. Nature conservation benefits by careful planning based on all existing knowledge regarding biodiversity, including threatened species and natural areas on all spatial and temporal scales.

Knowledge on the species level creates a broad basis for theoretical and practical actions in conservation biology. A growing number of species cannot adapt to a changed environment. Value-laden determination of species into those which are rare and threatened helps to concentrate on the most important species groups in conservation management. Rare species are often at risk of becoming extinct, either because of human activity or through local ecological interactions, natural disasters, pollution, climatic fluctuations or loss of the few suitable habitats (Vellak et al 2007).

The possible causes of rarity can be classified into two broad categories: natural rarity and rarity due to unsuitable human activity. Broad natural rarity causes are classified according to their geographic range, habitat specificity and local population size (Rabinowitz 1981). Life-history trait patterns of different species, however, are largely context dependent (Pilgrim et al 2004) and no clear differences between the traits of rare and common vascular plant species were found (Bevill & Louda 1999).

Regional rarity can be caused by local climate in the present and past, geographical and ecological conditions, as well as historical and current land use. Rare species can be local relicts from warmer climate periods; for example, several neotropical bryophyte species were found in Western Europe (Frahm 2003). In the Northern Hemisphere natural rarity is obviously related to post-glacial dispersal history where many dispersal-limited species are still migrating back to their previous distribution areas from their ice age refugia (Svenning et al 2008).

Shortage of suitable habitat can cause rarity in many species (Wiklund 2002; Vanderpoorten & Engels 2003; Pilgrim et al 2004). The presence of particular rare habitat types determines the distribution of species associated only with this habitat type. Some of these types can be rare in a particular region for natural reasons. Rare species are usually also more specialized to one habitat type (Birks et al 1998; Heinlen & Vitt 2003), for example, rare bryophytes can often be found only on one type of substrate (Ingerpuu & Vellak 1995). Other habitat types might be rather common in principle, but their late successional stages might be rare due to overwhelming management activities.

Small population sizes are caused by a specific evolutionary background and life-history traits. The evolutionary nature of rarity can become evident if we evaluate the proportion of rare species in different taxonomical units. Species-rich vascular plant families tend to contain more rare species in general (Lozano & Schwartz 2005). On the basis of British vascular plant flora, however, it has been shown that some families include more rare species than others that are of almost the same size (Pilgrim et al 2004). Thus, some evolutionary lineages probably have traits which might prevent those species from becoming widespread and abundant.

Anthropogenic rarity has developed during a lengthy period of social community. Human population density and species diversity tend to be correlated (Pautasso & McKinney 2007). Neglecting or changing traditional forest and grassland management to more intensive logging or agricultural use can render several species locally rare (Mäkipää & Heikkinen 2003; Zechmeister et al 2003), or can cause their replacement with expansive species (Söderström 1992). In Europe many species are threatened due to lack of suitable management of agricultural landscapes (Pykälä 2000). Moderate human land use like grazing of domestic animals, mowing meadows or selectively cutting forest has a history in Northern Europe for thousands of years (Pärtel et al 1999; WallisDeVries et al 2002; Pärtel et al 2007). This process has caused an increase of human-tolerant species and a decrease in human-sensitive species (Pejchar et al 2007). Thus, local flora has adapted to such moderate disturbances.

Unfortunately, the conservation assessment of different taxonomic groups is unequal. The term “rarity” may have different meanings with species from different taxa (e.g. vascular plants and bryophytes). New approaches in conservation biology emphasize the actual need to look more carefully for the geographic variation of nature and to investigate all kinds of species groups, including bryophytes (Lomolino et al 2005). Thus, research discovering the reasons for rarity of vascular plants and bryophytes together can lead to more efficient nature protection.

Conservation value and status of species is expressed in the Red Lists, legal act lists, lists to determine conservation management efficiency, etc. The evaluation of rareness depends on evaluation criteria and on the size of the territory. Rare species are commonly determined for a certain country (Witte & Torfs 2003) and thus a sparsely distributed species, evaluated as rare in a small country, may not be rare in a larger country, skewing the counting process. As a result, higher standards are set for conservation in smaller countries. Rare species are considered to be endangered by a particular factor on a particular scale, and active or passive means must be taken to stabilize or improve their status. Red Lists describe the degree of threat of a species (low number of individuals or localities found), and the apparent major reasons for its decline (Hilton-Taylor 2000). Although natural rarity and endemism remain as the basic concept for conservation, sometimes it is too narrow.

Using all such listings of threatened and rare species, it is possible to have a wider concept of those needing conservation, by means of further grouping and prioritization. There is probably an optimal level of resolution between focusing on a few subjectively selected „hot” species and the total list of species of conservation interest. One solution can be an approach focusing on groups of species that could be subjected to similar conservation means. Those groups should aim to integrate the general information about the possible factors and mechanisms behind the real or potential decrease of the abundance and distribution area of those species. There are still, however, rather few studies that have attempted to use a grouping approach to the flora of certain regions for

conservation purposes (Rabinowitz et al 1986; Médail & Verlaque 1997; Blanca et al 1998; Pitman et al 1999; Lozano et al 2003; Broennimann et al 2005; Burgman et al 2007; Barker & Fish 2007).

Most of the species groupings for conservation are based on a general scheme of rarity offered by Rabinowitz (1981) in which she combined three rarity criteria: restricted distribution, requirement for specific rare habitat, and small population sizes. These three criteria can produce eight combinations; seven of them are rare at least according to one criterion. It is important to note, however, that human impact is not specifically considered in the Rabinowitz system. In addition, knowledge about rarity in itself remains too narrow to organize efficient biodiversity preservation. Thus an integrated approach to group species based both on natural and anthropogenic causes of rarity might be more successful. Nevertheless, uneven distribution of rare species and their habitats need both spatial and temporal dimensions to estimate where and when our actions in nature protection appear to be most successful.

Ongoing global climate change and dramatic shifts in land use have created novel situations for conservation. Therefore taking into account various threats and causes of rarity, we need additional knowledge of how biodiversity conservation correlates with the network of protected areas (e.g. see Deguise & Kerr 2006). Uneven distribution of biodiversity features and human land use requires conservation management which takes into account the spatial dimension. Depending on scale, we can use dot, line or polygon phenomena to solve conservation questions. Polygons in the form of protected areas have been used as an efficient and plain tool for nature conservation. The number of species with conservation need, however, has increased to a level where there is no longer time or resources to establish protected areas for each individual threatened taxon (e.g. see Wilson et al 2007). Since there is a continuous improvement in our knowledge in conservation biology, there is also ongoing need for improving the existing network of protected areas. The protected area system is not a single but still a principal component of conservation. Ideally, protected areas should “cover” the full variety of biodiversity.

Protected areas are essential for conservation strategies (Bruner et al 2001). Rare species are often used to estimate the efficiency of the protected areas system (McKinney 2002). These species allow a more exact understanding of how to organize nature protection spatially. The World Conservation Union (IUCN) has set a goal to cover 10% of every country by protected areas (Rodrigues & Gaston 2001). Currently this goal has been met in many regions, but a global analysis identified that 12% of terrestrial vertebrate species are still not covered by any protected area at all (Rodrigues et al 2004). On the other hand for example boreal forest landscapes need not only what ever type of protected areas but strict protection in the same amount (Löhmus et al 2004). The Global Strategy for Plant Conservation under the Convention on Biological Diversity emphasizes the importance of documenting plant diversity and species distribution in protected areas (Lowry & Smith 2003). The Strategy sets measurable and achievable targets for the year 2010. The primary goal is to

cover at least 60% of threatened species in the world with *in situ* protection (mainly in protected areas), and at least 50% of areas valuable for plant diversity at the local or national level. Similarly, the coverage of 60% of threatened plant species by protected areas might be too “soft” in many areas with long traditions in nature conservation (e.g. Northern Europe) because current threats to species can be quite different from those in the past.

The quantified proportion of conservation goals (percent of area, number of species, spending, etc.) might act as easily usable measurements but real content of these numbers in the meaning of conservation will only become evident with additional research work and proper management. Setting conservation targets by these quantitative measurements does not give exact information for managers to achieve the desired effect in biodiversity conservation. Such fixed numeric goals, however, might be too robust. Existing conservation area networks need careful management based on exact knowledge of how large an area is needed to afford protection to a whole set of species. The approach analyzing effectiveness of protected areas is called Gap Analysis. This approach is gaining increasing popularity in conservation planning (Pressey & Cowling 2001), partly due to the respective USA program which started at the end of the last century (Jennings 2000). This case is especially important when we use conservation needed species lists in which two types of species rarity - natural and human induced - are simultaneously combined. Systematic conservation planning and protected area selection for separate species allows easier achievement of the desired results, for example, the minimum number of areas that cover a particular group of species. The conservation task becomes more complicated when one wants to protect conservation needed species with different conservation management approaches. Knowing reasons for species rarity and how these ideas are integrated into conservation management through protected areas remains important.

Historically, establishment of protected areas and organizing nature protection started on a national scale. Although national scale studies have special interest because of detailed local information and direct conservation knowledge for state institutions, conservation management requires also a wider picture on larger regional scale. A regional approach allows overcoming gaps and biases in the representation of biodiversity because the knowledge of protected areas system must consider biodiversity features not only on the local/national level, but also in neighbouring areas. A good example of the application of qualitatively new knowledge for planning nature protection on a regional scale exists on the Iberian Peninsula (García et al 2002; Araújo et al 2007). Regional studies will obtain good results when the whole territory is uniformly covered with information. Neighbouring states with an almost similar level of natural investigations are suitable for such regional studies. However, the spatial aspect in conservation cannot be considered without including temporal trends.

Temporal aspects in conservation might be highly informative since focus and traditions have changed considerably over past decades. Several conserva-

tion approaches contain time scale as an important determinant factor for many processes, for example theories about species pools, community successions, or landscape heterogeneity. However, the temporal aspect remains important in the protected area system and development of ideas about conservation.

The establishment of protected areas began a century ago, but the principles of their establishment have changed significantly. The focus in earlier periods was on recreation and landscape beauty, extending gradually to conservation of rare species and, more recently, nature management, restoration and support to ecosystem function (Anon. 1944; Bengtsson et al 2003; Boitani et al 2008). Gap analysis of protected areas system is well-known from the point of view of spatial distribution. Analogous analysis is useful also for the temporal scale. Ideally, the effectiveness of the protected area network should increase in time. For example, a comparison of effectiveness of reserves from Central Florida before a recent land-acquisition and now, show that many plant and animal species are substantially better protected (Turner et al 2006). Thus, by analyzing historical and current coverage of biodiversity in protected areas, we can measure how influential conservation decisions have been in the past. Knowing the history of the effectiveness of protected areas can assist careful planning for the future.

AIMS AND HYPOTHESES

The purpose of this study was to examine fundamentals of plant species protection. Our research is focused on plant species rarity problems and their coherence with protected areas in spatial and temporal scales. The objectives of this thesis were as follows:

1. To develop a synthetic approach to determine causes of plant rarity in a particular region and to group plant species according to different conservation aspects. We hypothesize that a synthetic approach combining both natural and anthropogenic causes of rarity results in a functional system both for basic and applied conservation biology (**Paper I**)
2. To determine if different groups of vascular plant species with particular conservation need require a different number of protected areas to cover an equal proportion of its species and to determine if species groups have been covered by protected areas differently throughout the last century (**Paper II**)
3. To determine, a) whether the reasons of rarity of regionally rare moss species are caused by their taxonomy, life history traits and/or specific ecological demands and, b) do rare mosses inhabit other types of habitats and substrates than frequent mosses (**Paper III**)

MATERIALS AND METHODS

The study used two model areas with different sizes – one for national scale and another for regional scale research.

Our study of protected areas and threatened species conservation included the total area of Estonia (N 57° – N 59° and E 22° – E 24°, 45,000 km²). This is a very good model for nature conservation studies because of its unique natural conditions - a large number of habitat types with rich, well-studied flora within a small country. The main abiotic parameters vary widely. The bedrock is half sandstone (south), half limestone (north). The climate has both coastal (west) and inland (east) characteristics.

The study area to explore the spatial distribution of rare bryophytes covers the territory of three Baltic countries (N 59° – N 53° and E 20° – 28°) with the area approximately 175,000 km². Specific features between countries appear mainly in climate and in bedrock. The Baltic countries are characterized by diverse ecosystems which are changing rapidly due to human activity.

Grouping and prioritization of vascular plant species for conservation

The national list of the vascular plant species with conservation need was compiled on the basis of the lists of legally protected vascular plant species of Estonia (Kukk 1999), plant species in the Red Data Book of Estonia (Lilleleht 1998), and from Annexes of the EU Habitats Directive (1992) found in Estonia. We excluded all infraspecific taxa and microspecies with no clear taxonomic status from the genera *Alchemilla*, *Crataegus*, *Euphrasia*, *Hieracium*, *Pilosella*, *Rosa* and *Taraxacum*. We applied the synthetic grouping of vascular plant species with similar conservation need. We separated four natural causes of rarity (restricted global distribution, restricted local distribution, very rare habitat, small population size) and the four most important anthropogenic causes of rarity (dependence on grassland management, dependence on local natural and human-induced disturbance, dependence on traditional extensive agriculture, possible threat due to collecting). We analyzed the co-occurrences of different conservation characteristics by Principal Component Analysis (PCA) with eight characteristics as factors and 301 species as cases. Fisher Exact test was used to discover associations between factor pairs.

Evaluation of past and present effectiveness of protected areas

The model area is covered with a well-established system of ecological regions (Lippmaa 1935; Laasimer 1965). The landscape structure on a national scale has

been relatively unchanged during the last century (Palang et al 1998). The development of protected areas over time demonstrates the similar dynamics between Estonia and the whole of Europe. We gathered the presence/absence data of species in protected areas from various published and unpublished sources. In total we had 33 spatially independent protected areas of various sizes (17...36 885 ha). During the analysis of the protected areas system Gap Analysis we used 289 from 301 species because some taxonomic units were not described on the same level in every protected areas plant lists.

A species-accumulation function describes the expected accumulated number of various species which were found within a geographical region and the type of effort that was made (sample, time, etc.) (Diaz-Frances & Soberon 2005). In order to study present coverage of different species groups by protected areas we used these species' accumulation curves (Gotelli & Colvell 2001; Colwell et al 2004). These graphs show the rise in the number of species covered by protected areas, along with the increasing number of protected areas. Species accumulation curves with 95% confidence limits were constructed using a randomization algorithm in the software EstimateS (Colwell 2005). Changes in plant biodiversity protection on a temporal scale were analyzed with the help of the establishment years of protected areas (ranking from 1910 to 2004). The protected area network was increased by new protected areas 17 times during the last 100 years. For each period we found the number of species within particular species groups that were actually covered by particular protected areas present at that time. On this basis we constructed the actual curve of species protection in time. We compared the actual curve with the theoretical curve. The theoretical species accumulation curve was based on the number of protected areas achieved during a particular period, selected randomly from the total list of protected areas (not considering actual year of establishment). If these two curves (actual and theoretical) differ, it means that some species groups were preferred in the establishment of protected areas at some time period. The difference between these two curves was determined by the Kolmogorov-Smirnov two-sample test (Zar 1996). Significance levels were adjusted by sequential Bonferroni procedure in multiple testing situations (Holm 1979).

Studying regional moss rarity

The list of moss species of the Baltic States was compiled on the basis of the bryophyte flora of the Baltic States (Äbolina 1994, 2002; Bambe 2002; Ingerpuu et al 1998; Jukoniene 1996, 2003; Vellak et al 2001). Life span (short- or long-living) was conformed to the classification of During (1992). Several ecological catalogues have been compiled for expressing specific demands of bryophyte species all over Europe (Düll 1991; Hallingbäck 1996; Dierßen 2001; etc). For this study, light, substrate pH, humidity, continental and temperature index of species according to Düll (1991) were used. Some supplements were

made according to Hallingbäck (1996). We compared only species with contrasting frequencies – frequent and rare. In the first step the list of all species occurring in these three countries was compiled. From this list two species lists were extracted: species that occur in all three countries and species that occur only in one country. Species that occur in two countries were excluded. The next step was to select the species for our analysis according to the frequency estimations in flora of all three countries. We compiled three groups of species: 1) frequent species that occur in all three countries and are estimated in flora only as ‘common’, ‘very common’, ‘frequent’ or ‘very frequent’; 2) rare species that occur in all three countries and have up to 12 (included) localities in every country, and 3) very rare species that occur only in one country and have up to 12 (included) localities in this country. We excluded all other species because their frequency in the whole region is uneven, intermediate or unknown and sound interpretation cannot be made. Altogether 184 moss species satisfied the selection criteria and were included in the analyses. For evaluation of local ecological conditions on the species distribution, the main substrate type (soil or other substrata), number of possible substrata, and prevailing community type (forest or open community) were obtained for every species from moss flora of the three Baltic States. The Chi-square test was used to evaluate if family affiliation, species life history parameters, preferences for substrate and community type were distributed similarly in frequency groups. The one-way ANOVA was used to investigate differences in ecological indexes between frequency groups and between different countries inside the very rare species group. The differences between the means of dependent variables were compared with the Tukey HSD test. All differences were considered significant at the level $P < 0.05$.

RESULTS

Grouping and prioritization of vascular plant species for conservation

The distribution of the conservation characteristics among the species of conservation need varied a lot (Table 1). *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 on grassland management* (32%), *threat due to collecting* (31%), and *always having small populations* (21%). The least common conservation characteristic was *very rare habitat*, representing 7% of the species. Other less frequent conservation characteristics were *dependence on natural or human-induced disturbance* and *dependence on traditional extensive agriculture*, both associated with 10% of the species.

Table 1. The synthetic grouping of vascular plant species with conservation need combining natural and human-induced rarity (Pärtel et al 2005).

Groups	Groups (% of species)	Description	Examples
Natural causes of rarity			
a) Restricted global distribution	38 %	species found only in Europe	<i>Allium ursinum</i> , <i>Cephalanthera rubra</i> , <i>Serratula tinctoria</i>
b) Restricted local distribution	28 %	in less than 5% of 100 km ² grid cells	<i>Botrychium matricariifoli</i> , <i>Juncus squarrosus</i> , <i>Trifolium campestre</i>
c) Small population size	21%	approximately less than 300 mature individuals	<i>Agrostemma githago</i> , <i>Dactylorhiza cruenta</i> , <i>Taxus baccata</i>
d) Vary rare habitat	7 %	species specialists in very rare habitat	<i>Asplenium ruta-muraria</i> , <i>Cochlearia danica</i> , <i>Pinguicula alpina</i>
Human-induced rarity			
e) Dependence on grassland management	32%	species on semi-natural grasslands	<i>Gladiolus imbricatus</i> , <i>Poa alpina</i> , <i>Thalictrum lucidum</i>
f) Dependence on local natural and human-induced disturbance	10%	species whose regeneration takes place in disturbed forest areas	<i>Dianthus arenarius</i> , <i>Oxytropis pilosa</i> , <i>Pulsatilla patens</i>
g) Dependence on traditional extensive agriculture	10%	species which are rare due to new technologies in agriculture	<i>Bromus secalinus</i> , <i>Cardamine hirsuta</i> , <i>Cuscuta epilinum</i>
h) Possible threat due to collecting	31%	species potentially threatened by collection	<i>Cypripedium calceolus</i> , <i>Iris sibirica</i> , <i>Lycopodium clavatum</i>

Principal Component Analysis on conservation characteristics revealed that the first axis described 17.2% and the second axis 16.9% of the total variation. On the ordination diagram, all conservation characteristics show very little overlap. There was just one significant positive association between conservation characteristics: *restricted local distribution* and *small size of populations* (Fisher exact test, two-tail, $P = 0.026$). Significant negative associations were more common: *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 on grassland management* ($P = 0.037$), *threat due to collecting* and *dependence on traditional 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.

Evaluation of past and present effectiveness of protected areas

Species accumulation curves showed that different groups of plant species with conservation need had different spatial coverage by protected areas (Fig. 1). The 95% confidence limits of these curves remained wide, often exceeding the number of 33 protected areas (Fig. 1b, d, f). For species that were rare due to natural reasons, almost twice as many protected areas were needed to cover 60% of its species, compared with the species that require proper human management. Consequently, a single accumulation graph might overlook some rarity types. We suggest that during modification of a protected area network, naturally rare species, especially those with restricted local distribution (Fig. 1b) or requiring rare habitat type (Fig. 1d) should be given most consideration.

Protected areas had not been founded evenly during the last century. The temporal trend in the coverage of different species groups by protected areas always varied from the random (Fig. 2). There were two groups with strongly contrasting conservation history. Establishment of protected areas for species requiring very rare habitats was historically much more strongly covered than expected by chance (Fig. 2d). In contrast, species that depended on traditional extensive agriculture were generally neglected in the protected areas in earlier times (Fig. 2g).

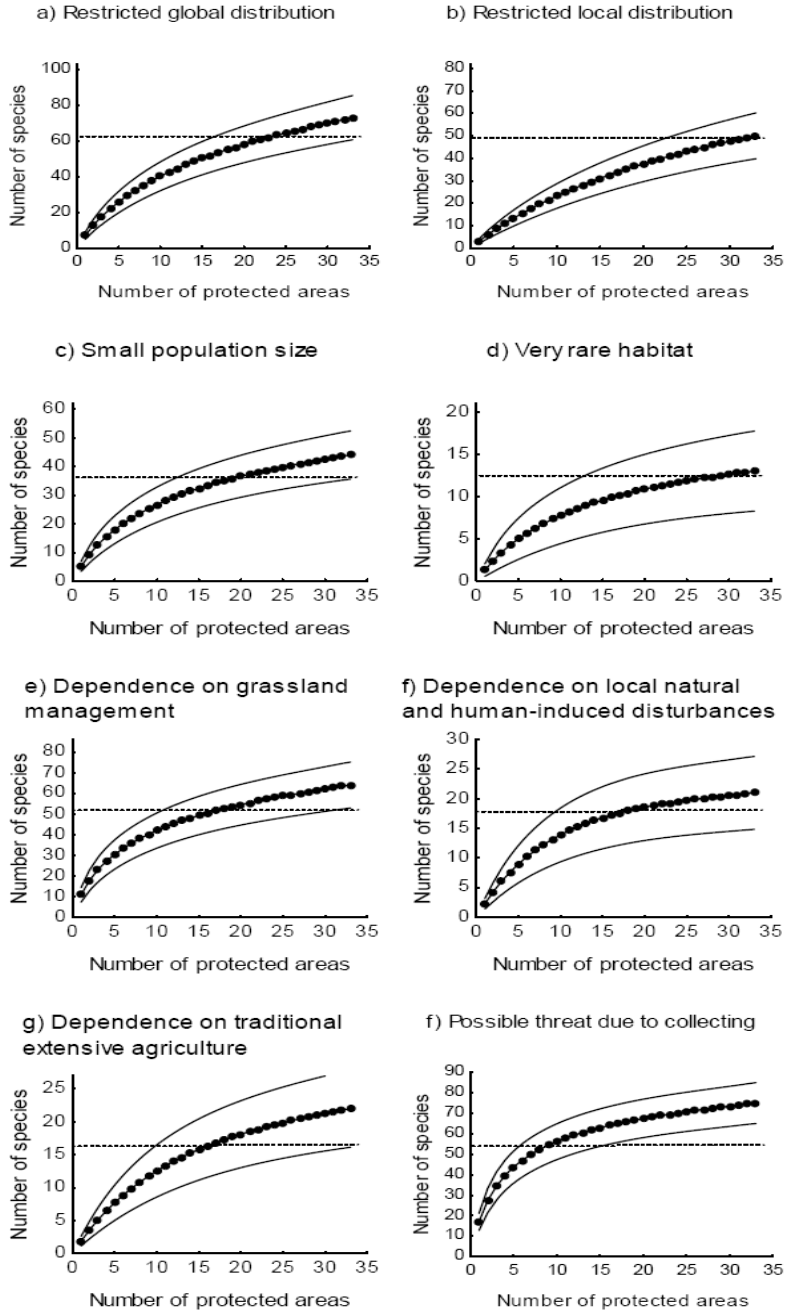


Figure 1. Species accumulative curves over increasing number of protected areas for groups of species of natural causes of rarity (a–d) and human-induced rarity (e–h). Average values with 95% of confidence limits. 60% of coverage, suggested by the Global Strategy of Plant Conservation, is indicated by horizontal lines (the vertical axis is covering the full 100%) (Vellak et al in press)

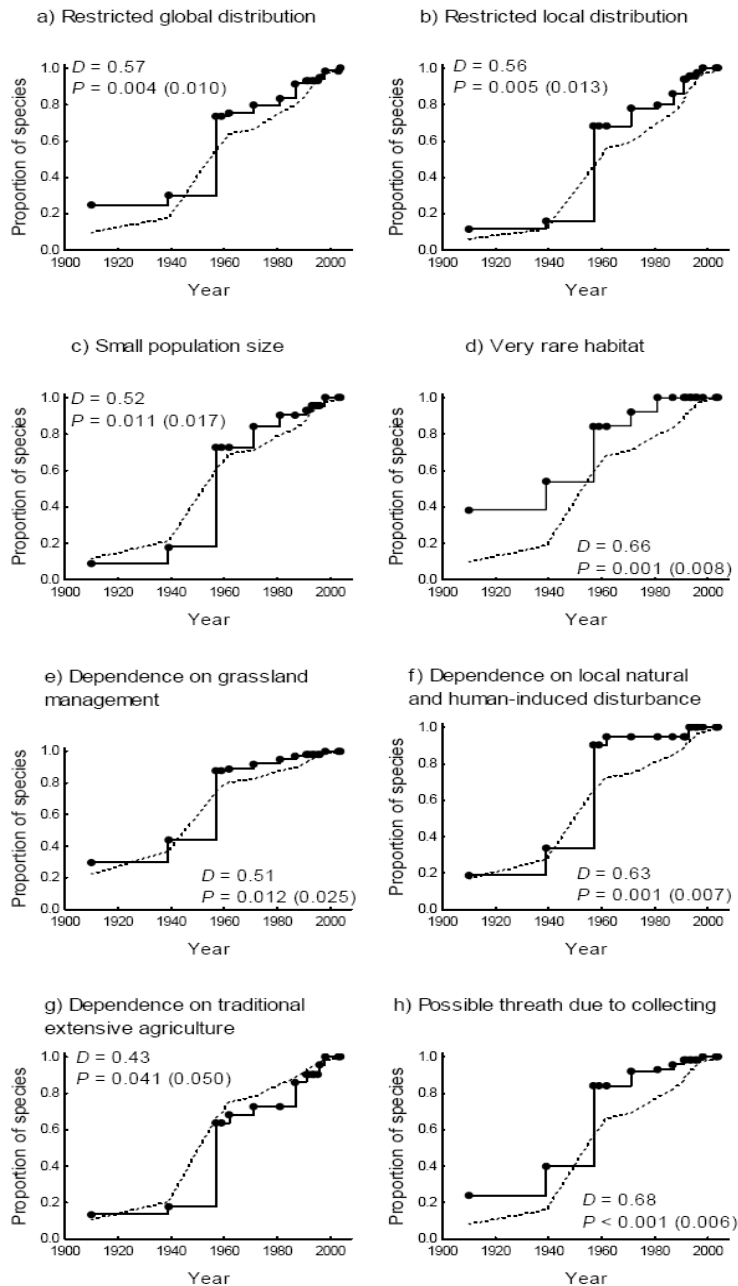


Figure 2. Temporal dynamics in coverage by protected areas for groups of species of natural causes of rarity (a–d) and human-induced rarity (e–h). Dots with step linkage indicate actual coverage and dashed line theoretical, considering the number of protected areas but not their establishment sequence. Statistics from the Kolmogorov-Smirnov test (D) with P value are reported. Critical P values according to the sequential Bonferroni correction are in parentheses. (Vellak et al in press).

Studying regional moss rarity

The whole moss flora of the Baltic States contains 483 species; 277 species occur in all three countries and 93 species occur only in one of them. The group of frequent species includes 45 species, 2) the group of rare species includes 61 species and 3) the group of very rare species includes 78 species (46 species from Estonia, 20 species from Latvia and 12 from Lithuania). The analyzed species belong to 30 families, whereas only seven families include more than 10 species. There was a significant difference in the distribution of families between the frequency groups (Chi-square = 30.94, $P < 0.01$, $df = 14$). Families *Grimmiaceae* and *Pottiaceae* are characterised by the highest number of species in the group of very rare species; *Sphagnaceae* was lowest.

Of life history parameters, only life span was significantly differently distributed between frequency groups (Chi-square = 13.18, $P < 0.001$, $df = 2$). The percentage of species with a short life span was highest in the group of very rare mosses, while the percentage of species of long life span was highest in the group of frequent mosses.

Species preferences for substrate type as well as for number of possible substrata were also significantly differently distributed (Chi-square 9.73, $P < 0.01$, $df = 2$ and Chi-square = 17.28, $P < 0.01$, $df = 4$ accordingly). Although the majority of analyzed species inhabit soil, the percentage of non-epigeic species was the highest in the group of very rare species. Rare species are mainly specialized to one type of substrate. Ecological indexes in the group of rare mosses had significant differences only in temperature indexes ($F_{1, 182} = 5.69$, $P = 0.005$). The species occurring only in Lithuania prefer the highest temperature. Species inhabiting different community types were significantly differently distributed among frequency groups (Chi-square 26.66, $P < 0.001$, $df = 4$). The majority of frequent species inhabit forests, while the majority of rare species inhabit open communities. Frequency groups were differently distributed also according to the EU habitat type groups.

Significant differences appeared according to the substrate pH and humidity preferences ($F_{1, 182} = 4.67$, $P = 0.011$; $F_{1, 182} = 8.49$, $P < 0.001$ accordingly): rare mosses prefer substrata with higher alkalinity and higher humidity.

Comparing ecological indexes in the group of rare mosses occurring only in one country, significant differences were found only according to temperature indexes ($F_{1, 182} = 5.69$, $P = 0.005$).

The percentage of species with a short life span was highest in the group of very rare mosses, while the percentage of species of long life span was highest in the group of frequent mosses.

DISCUSSION

Since causes to maintain biodiversity are linked to processes acting at various scales, nature conservation and management should also take place at different spatial and temporal scales. Accordingly, different analyses which manage biodiversity conservation problems include special attention to spatial and temporal influences. Three main spatial processes that can greatly influence biodiversity are changes in landscape heterogeneity, biotic interactions and disturbance (Gardner & Engelhardt 2008). On the other hand new approaches in conservation biology on the species level emphasize the actual need to look more carefully for the geographic variation of nature and to investigate all kinds of species groups, including bryophytes (Lomolino et al 2005).

From a conservation point of view it is important to know the reasons for rarity in a particular region and the local hot spots for rare species, since this enables the preservation of the whole phylogenetic diversity in the region (Meffe & Carroll 1994). Although rare and threatened species concepts with their theoretical and practical outcomes have certain value in biodiversity preservation, the conservation activities include more possibilities. Establishment of protected areas has been a powerful tool for conservation. The combination of species-level data with the protected areas approach has been most appropriate to evaluate protected area effectiveness (Brooks et al 2004). At the same time we acknowledge that wider perspectives have emerged in the sense of diversity-environment relationship to understand more exactly plant diversity distribution (Zobel & Pärtel 2008) and integrate this knowledge into conservation practice. Thus, conservation research can be successful if we consider different time and space dimensions.

Traditionally, the starting point in plant conservation has been the identification of rare species (mostly defined by low number of localities where the species is found). After that, the possible causes of rarity and future threats can be identified. In reality, the rarity of most species is the outcome of multiple processes, frequently either unknown or overlooked. The traditional approach is certainly justified in most cases, but it can be complemented by the additional approach proposed in this thesis. We suggest that the planning of conservation measures should start with cases where active conservation is possible, i.e. in cases when human influence is the most probable force behind rarity; thereafter we can consider the remaining species according to most probable cause of rarity.

The possible causes of rarity can be classified into two broad categories: natural rarity and rarity due to unsuitable human activity. There is probably an optimal level of resolution between focusing on a few subjectively selected species of special interest and the total list of species of conservation interest. There are still, however, rather few studies that have attempted to use a grouping approach to the flora of regions for the purpose of conservation (Rabinowitz et al 1986; Médail & Verlaque 1997; Blanca et al 1998; Pitman et

al 1999; Lozano et al 2003; Broennimann et al 2005; Barker & Fish 2007; Burgman et al 2007). In the case of vascular plants, conservation prioritisation frequently relies on the experience and intuition of conservation biologists (Sutherland et al 2004). The current approach might give a more objective basis for prioritization, since one can assume that the more conservation characteristics a species has been assigned, the higher is the overall risk that the species will become extinct in the particular region under consideration. According to that, 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, confirming or challenging subjective decisions. On the list of vascular plant species of conservation status in Estonia, each species was assessed on the basis of the eight qualitative conservation characteristics. This categorization allowed us to form two large groups – one for natural rarity and another for human induced rarity.

From the natural rarity groups a smaller share of species with conservation need (7%) depends on the presence of particular rare habitat types. Some of these types can be rare in a particular region for natural reasons: rocky habitats, oligotrophic lakes or floodplain and escarpment-associated forests in Estonia (cf. Paal 1998). For example, the protection of rare moss species could be promoted through conservation of natural open communities as calcareous fens and coastal and water habitats. Other habitat types might be rather common, but their late successional stages might be rare due to overwhelming management activities. The subsequent 10% of species with conservation need have very small populations, evidently for evolutionary and historical reasons. For instance, a species might be outside its optimal geographical distribution, or 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.

Species belonging to the human-induced rarity groups have often had a low priority in conservation. For example, weeds connected to traditional agriculture have been left aside from legal protection. On the other hand, species suffering under direct human activity – e.g. collecting beautiful flowers - have received sufficient attention. Almost half (49%) the species with conservation need can be improved by proper management. Conservation actions mean support for conservation management, such as traditional grassland management and agriculture, and prescribed forest disturbances. Public education is an important aspect as well. An additional 18% of species are threatened by collecting; better legal regulation and public education can help here. Since the cause-effect relationship is relatively evident in management and threat due to collecting, one can expect that either supported management or restrictive regulation will result in a relatively rapid positive effect on local biodiversity.

The goal of the Global Strategy of Plant Conservation is to cover 60% of threatened plant species by protected areas by the year 2010 (Lowry & Smith 2003). We propose that 60% should be covered for each species group representing different causes of rarity. We explored how effectively protected areas cover plant species of different natural and anthropogenic causes of rarity, including both the historic development during the last 100 years and the current pattern of protected areas. Our model showed that the average number of protected areas required to cover 60% of species of conservation interest ranged from 9 to 33. The shapes of species accumulation curves, however, indicate that the number of protected areas must rise quickly if we want to conserve biodiversity more effectively, for example, protecting 80% – 95% of species. We also noticed wide confidence intervals for the species accumulation curves. The upper confidence interval showed that careful selection of protected areas, although a small number, might result in a high number of protected species (Primack 1993). In reality, however, protected areas are sometimes placed in regions which are less diverse but easy to set aside (Pressey et al 1996). For this scenario the lower confidence interval is used to estimate the number of protected areas needed for the 60% goal. Our research results emphasized that species that are rare due to natural causes need almost twice as much protected area to cover 60% of the species compared with those species which depend on human management. This fact supports the idea that these types of rare species require exact spatial planning. Therefore, naturally rare species can act as biodiversity indicators for gap analyses of protected areas.

The protected areas network in Estonia is a mixture of natural and semi-natural ecosystems. Species distributions have adapted to the extensive land use of the past. In recent decades intensive land use has replaced the traditional patterns but due to extinction debt, human management-dependent species still exist in many places (Helm et al 2006; Moora et al 2007). Although species that are threatened due to lack of suitable management (extensive agriculture and forestry) are still widespread and thus need less protected area to cover 60% of the species, this situation might change in coming decades when the extinction debt will be paid.

During the last century, naturally rare species and species dependent on management were not treated equally when protected area networks were designed, indicating the sensitivity of these groups to changes in the concepts of conservation policy (Maran 2005). For example, in the past, species with very rare habitat requirements were given most consideration in the establishment of protected areas. Each particular cause of rarity can describe a group of species that need similar conservation measures. Thus, the same strategies can be used for several species, not just for individual species. At the same time, species which needed traditional extensive agriculture were initially neglected. We suggest that synthetic species grouping according to different rarity causes is a useful tool in gap analysis of protected areas.

As a practical suggestion, 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 & Marrs 2003). Identifying species with similar conservation need allows one to work with species groups 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.

Time scale has become especially important recently, as it is possible that climate warming will affect the results of conservation planning. Some rare species can develop more successfully and become common species; some common species with more northern distribution might become rare. Thus conservation needed species lists and conservation planning should be checked after established time intervals and be adaptive on a temporal scale.

The shortage of floristic investigations in many regions has been noted as a main obstacle for maintenance of bryophyte protection in general (Cleavitt 2005). The Baltic States could serve as a good example for evaluating reasons of rarity inside one region as we have recently published moss flora and lists. The total number, as well as the number of very rare moss species diminishes across the three countries from north to south, being lowest in Lithuania. Even the number of native vascular plants is lowest in Lithuania (Vellak et al 2007). In general this might be explained by more diverse natural communities in Estonia and Lithuania's more arable landscapes.

Although habitat shortage explains much of the rarity among mosses, there are several species that have preferences for relatively scarce habitats, but are not rare. Species with good dispersal and establishment ability give them an advantage in patchy environments (Herben & Söderström 1992; Laaka-Lindberg 1999). Even life history parameters can be associated with habitat shortage. The percentage of species with a short life span was found to rise with rarity level. Short life span is characteristic of species belonging to life strategy groups that use habitats with short duration (During 1992). Such unstable habitats depend mainly on small-scale disturbances and do not cover large areas in comparison with stable habitats.

When comparing different regions and the species characters in the very rare mosses group, along with the availability of suitable substrata, the relevance of local ecological conditions is also important. The country-specific rare species differ in relation to temperature and substratum alkalinity. The rare moss species present only in Lithuania prefer higher temperature. The lack of these species in Latvia and Estonia is obviously caused by lower winter temperatures in these countries. Moss species rare in the Baltic States are restricted mainly with one substratum type and prefer alkaline conditions. These results are in correspondence with study in forests where the results demonstrated that for bryophyte conservation the direct consideration of substratum diversity could be more effective than protection at habitat level (Lõhmus et al 2007).

Moss distribution along three Baltic countries and conservation needed vascular plant distribution in Estonia's protected areas system demonstrates explicitly that a group approach to conservation of rare species has theoretical and practical importance.

CONCLUSIONS

Systematic conservation planning acts on different levels of biodiversity and on different spatial and temporal scales. Concepts of rare species and protected areas allow the estimation of conservation efforts undertaken by society.

1. We provided a synthetic concept to group species with different conservation need using both information about the natural rarity and human management requirements; we proposed eight groups for vascular plants. Grouping and prioritizing of conservation needed plants in a synthetic way seems to be a successful conservation tool for future theoretical research work and for practical conservation management. Combining species with the same conservation management and planning activities helps to increase nature protection efficiency. Although our approach was elaborated on the national scale in Northern Europe, our efforts have been acknowledged widely. We also highlighted that some plant diversity might be lost because of underestimation of a particular threat, e.g. lack of moderate forest disturbances both in managed and protected forests (Reier et al 2005).
2. Integrating the two approaches – use of species accumulation curves and grouping of species with similar conservation needs – is a feasible way to study the efficiency of protected areas in biodiversity conservation. Plant species that are naturally rare (due to restricted global or local distribution, always small populations or requiring very rare habitats) need more, almost twice as much, protected area to be covered, compared to plant species which are rare due to lack of suitable management. Historical data show high sensitivity of different species groups to decision making. Consequently, in conservation biology the lessons of history allow us to plan for the future. For example, synthetic species groups can effectively be used in monitoring schemes (Teder et al 2007) taking into account appropriate spatial units (Mander et al 2005; Roose et al 2007; Schmidt et al in press). Different species groups might not be uniformly covered by protected areas and we suggest that all major species groups should fulfil the target of 60% coverage by protected areas.
3. Our study explained that rarity of mosses on a regional scale is influenced more by ecological and life history parameters than by taxonomical affiliation. The habitats with characters preferred by rare mosses are in a minority in this region. The majority of rare moss species in the Baltic States are open habitat species limited to one kind of substrate and favoured by high alkalinity conditions. Characters of rare species present in only one country reflect soil alkalinity and mean temperature differences between these countries.

In summary, conservation planning processes depend largely on both spatial and temporal dimensions and on definition of focal species and their groups. Prioritized species groups allow better understanding of various conservation management principles and the integration of different conservation methods. Well-designed species groups can serve as an efficient conservation tool that

can produce more concise information than single rare species. Temporal scale analysis of conservational management has given evidence of similarities with cultural heritage preservation. Both need a clear understanding of the value of acknowledging time in conservation efforts. The temporal dimension of conservation planning allows consideration of historical conservation practice and assists planning for the future.

REFERENCES

- Ābolina, A. (1994) Latvijas retās un aizsargājamās sūnas. *Vides aizsardzība Latvijā*, 6, 3–24.
- Ābolina, A. (2002) Mosses of Latvia.
<http://latvijas.daba.lv/scripts/db/saraksti/saraksti.cgi?d=suunas&l=en>
- Anon. (1944) Nature Conservation and Nature Reserves. *Journal of Ecology*, 32, 45–82.
- Araújo, M.B., Lobo, J.M., & Moreno, J.C. (2007) The Effectiveness of Iberian Protected Areas in Conserving Terrestrial Biodiversity. *Conservation Biology*, 21, 1423–1432.
- Bambe, B. (2002) New and rare bryophyte species in Latvia. Pages 113–124 in E. Vimba, editor. *Retie augi*. Rīga.
- Barker, N., & Fish, L. (2007) Rare and infrequent southern African grasses: assessing their conservation status and understanding their biology. *Biodiversity and Conservation*, 16, 4051–4079.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., & Nyström, M. (2003) Reserves, resilience and dynamic landscapes. *Ambio*, 32, 289–396.
- Bevill R.L., & Louda, S.M. (1999). Comparisons of related rare and common species in the study of plant rarity. *Conservation Biology*, 13, 493–8.
- Birks, H.J.B., Heegaard, E., Birks, H.H., & Jongsdard, B. (1998) Quantifying bryophyte-environment relationships. Pages 321–331 in: J.W. Bates, N.W. Ashton, & J.G. Duckett, editors. *Bryology for the twenty-first Century*. Maney Publishing and the British Bryological Society.
- Blanca, G., Cueto, M., Martínez-Lirola, M.J., & Molero-Mesa, J. (1998) Threatened vascular flora of Sierra Nevada (southern Spain). *Biological Conservation*, 85, 269–285.
- Boitani, L., Cowling, R.M., Dublin, H.T., Mace, G.M., Parrish, J., Possingham, H.P., Pressey, R.L., Rondinini, C., & Wilson, K.A. (2008) Change the IUCN Protected Area Categories to Reflect Biodiversity Outcomes. *PLoS Biology* 6, 66.
- Broennimann, O., Vittoz, P., Moser, D., & Guisan, A. (2005) Rarity types among plant species with high conservation priority in Switzerland. *Botanica Helvetica* 115, 95–108.
- Brooks, T., da Fonseca, G.A.B., & Rodrigues, A.S.L. (2004) Species, Data, and Conservation Planning. *Conservation Biology*, 18, 1682–1688.
- Bruner, A.G., Gullison, R.E., & Rice, R.E. (2001) Effectiveness of parks in protecting tropical biodiversity. *Science*, 291, 125–128.
- Burgman, M.A., Keith, D., Hopper, S.D., Widyatmoko, D., & Drill, C. (2007) Threat syndromes and conservation of the Australian flora. *Biological Conservation*, 134, 73–82.
- Carrol, C., Noss, R.E., Paquet, P.C., & Schumaker, N.H. (2004) Extinction debt of protected areas in developing landscapes. *Conservation Biology*, 18(4), 1110–1120.
- Cleavitt, N.L. (2005) Patterns, hypotheses and processes in the biology of rare bryophytes. *Bryologist*, 108, 554–566.
- Colwell, R.K., Mao, C.X., & Chang, J. (2004) Interpolation, extrapolation, and comparing incidence-based species accumulation curves. *Ecology*, 85(10), 2717–2727.
- Colwell, R.K. (2005) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application.
<http://purl.oclc.org/estimates>

- Deguisse, I.E., & Kerr, J.T. (2006) Protected Areas and Prospects for Endangered Species Conservation in Canada. *Conservation Biology*, 20, 48–55.
- Diaz-Frances, E., & Soberon, J. (2005) Statistical Estimation and Model Selection of Species-Accumulation Functions. *Conservation Biology*, 19(2), 569–573.
- Dierßen, K. (2001) Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum Bibliotheca*, 56, 3–289.
- Düll, R. (1991) Zeigerwerte von Laub- und Lebermoosen. *Scripta Geobotanica*, 18, 175–215.
- During, H.J. (1992) Ecological classification of bryophytes and lichens. Pages 1–33 in J.W. Bates, & A.M. Farmer, editors. *Bryophytes and lichens in a changing environment*. Clarendon Press, Oxford.
- EU Habitats Directive. (1992) EU Habitats Directive (92/43/EEC). Consolidated Text. Office for Official Publication of The European Union. CONSLEG: 1992LOO43–01.05–2004.
- Farnsworth, E.J. (2007) Plant life history traits of rare versus frequent plant taxa of sandplains: Implications for research and management trials. *Biological Conservation*, 136, 44–52.
- Frahm, J.P. (2003) Climatic habitat differences of epiphytic lichens and bryophytes. *Cryptogamie Bryologie*, 24, 3–14.
- García, M.B., Guzmán, D., & Goñi, D. (2002) An evaluation of the status of five threatened plant species in the Pyrenees. *Biological Conservation* 103, 151–161.
- Gardner, R.H., & Engelhardt, K.A.M. (2008) Spatial processes that maintain biodiversity in plant communities. *Perspectives in Plant Ecology, Evolution and Systematics*, 9, 211–228.
- Glowka, L., Burhenne-Guilmin, F., McNeely, A.M., & Grünling, L. (1994) A guide to the Convention on Biodiversity. Gland, IUCN.
- Gotelli, N.J., & Colvell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391.
- Groom, M.J., Carroll, C.R., & Meffe, G.K. (2006) Meeting conservation challenges in the twenty-first century. Pages 661–699 in M.J. Groom, G.K. Meffe, & C.R. Carroll, editors. *Principles of Conservation Biology*. 3. ed. Sinauer Associates, Sunderland, Massachusetts.
- Hallingbäck, T. (1996) Ekologisk katalog över mossor. ArtDatabanken, SLU, Uppsala.
- Heinlen, E.R., & Vitt, D.H. (2003) Patterns of rarity in mosses of the Okanogan Highlands of Washington State: an emerging coarse filter approach to rare moss conservation. *The Bryologist*, 106, 34–52.
- Helm, A., Hanski, I., & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, 9, 72–77.
- Herben, T., & Söderström, L. (1992) Which habitat parameters are most important for the persistence of a bryophyte species on patchy, temporary substrates. *Biological Conservation*, 59, 121–126.
- Hilton-Taylor, C. (2000) 2000 IUCN Red List of Threatened Species. IUCN, Cambridge.
- Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70.
- Ingerpuu, N., Kalda, A., Kannukene, L., Krall, H., Leis, M., & Vellak, K. (1998) Eesti sammalde määraja, Eesti Loodusfoto, Tartu.
- Ingerpuu, N., & Vellak, K. (1995) The distribution and some ecological characteristics of Estonian rare bryophytes. *Arctoa*, 5, 143–148.

- Jennings, M.D. (2000) Gap analysis: concepts, methods, and recent results. *Landscape Ecology*, 15, 5–20.
- Jukoniene, I. (1996) Rare and threatened bryophyte species in Lithuania. *Botanica Lithuanica*, 2, 327–341.
- Jukoniene, I. (2003) Lietuvos kiminai ir žaliosios samanos. Botanikos instituto leidykla. Vilnius.
- Kukk, T. (1999) Eesti taimeistik. Tartu-Tallinn: Teaduste Akadeemia Kirjastus.
- Laaka-Lindberg, S. (1999) Asexual reproduction in a population of *Lophozia cilvicola* Buch in central Norway. *Plant Ecology*, 141, 137–144.
- Laasimer, L. (1965) Eesti NSV taimkate. Valgus, Tallinn.
- Lippmaa, T. (1935) Eesti geobotaanika põhihooni. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis)*, 28 (4), 1–151.
- Lilleleht, V. (1998) Red data book of Estonia. Threatened fungi, plants and animals. ETA Looduskaitse Komisjon, Tartu.
- Lomolino, M.V., Riddle, B.R., & Brown, J.H. (2005) Biogeography, Sinauer Associates, Sunderland, Massachusetts.
- Lozano, F.D., Saiz, J.C.M., & Ollero, H.S. (2003) Rarity and threat relationships in the conservation planning of Iberian flora. *Biodiversity and Conservation*, 12, 1861–1882.
- Lozano, F.D., & Schwartz, M.W. (2005) Patterns of rarity and taxonomic group size in plants. *Biological Conservation*, 126, 146–154.
- Lowry, P.P. & Smith, P.P. (2003) Closing the Gulf between Botanists and Conservationists. *Conservation Biology*, 17, 1175–1176.
- Lõhmus, A., Lõhmus, P., & Vellak, K. (2007) Substratum diversity explains landscape-scale co-variation in the species-richness of bryophytes and lichens. *Biological Conservation*, 135, 405–414.
- Lõhmus, A., Kohv, K., Palo, A., & Viilma, K. (2004) Loss of old-growth, and the minimum need for strictly protected forests in Estonia. *Ecological Bulletins*, 51, 401–411.
- Mander, Ü., Müller, F., & Wrška, T. (2005) Functional and structural landscape indicators: Upscaling and downscaling problems. *Ecological Indicators*, 5, 267–374.
- Maran, M., editor. (2005) Third national report to the Convention on Biological Diversity, Estonia. Estonian Ministry of Environment, Tallinn.
- McKinney, M.L. (2002) Effects of National Conservation Spending and Amount of Protected Areas on Species Threat Rates. *Conservation Biology* 16(2):539–43.
- Médail, F., & Verlaque, R. (1997) Ecological characteristics and rarity of endemic plants from southeast France and Corsica: implications for biodiversity conservation. *Biological Conservation*, 80, 269–281.
- Meffe, G.K., & Carroll, C.R. (1994) The Species in Conservation. Pages 50–77 in G.K. Meffe & C.R. Carroll, editors. *Principles of Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts.
- Meffe, G.K., Carroll, C.R., & Groom, M.J. (2006) What is Conservation Biology? Pages 3–25 in G.K. Meffe & C.R. Carroll, editors. *Principles of Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts.
- Menges, E.S. (2000) Population viability analyses in plants: challenges and opportunities. *Trends in Ecology and Evolution*, 15, 51–56.
- Moora, M., Daniell, T., Kalle, H., Liira, J., Püssa, K., Roosalu, E., Öpik, M., Wheatley, R., & Zobel, M. (2007) Spatial pattern and species richness of boreo-nemoral forest understorey and its determinants. – A comparison of differently managed forests. *Forest Ecology and Management*, 250, 64–70.

- Mäkipää, R., & Heikkinen, J. (2003) Large-scale changes in abundance of terricolous bryophytes and macrolichens in Finland. *Journal of Vegetation Science*, 14, 497–508.
- Norris, K. (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining population paradigm. *Applied Ecology*, 41, 413–426.
- Orians, G.H., & Groom, M.J. (2006) Global biodiversity: patterns and processes. Pages 27–61 in M.J. Groom, G.K. Meffe & C.R. Carroll, editors. *Principles of Conservation Biology*. 3. ed. Sinauer Associates, Sunderland, Massachusetts..
- Paal, J. (1998) Rare and threatened plant communities of Estonia. *Biodiversity and Conservation*, 7, 1027–1049.
- Palang, H., Mander, U., & Luud, A. (1998) Landscape diversity changes in Estonia. *Landscape and Urban Planning*, 41, 163–169.
- Pejchar, L., Morgan, P.M., Caldwell, M.R., Palmer, C., & Daily, G.C. (2007) Evaluating the potential for conservation development: Biophysical, economic, and institutional perspectives. *Conservation Biology*, 21, 69–78.
- 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, 525–31.
- Pärtel, M., Helm, A., Reitalu, T., Liira, J., & Zobel, M. (2007) Grassland diversity related to the Late Iron Age human population density. *Journal of Ecology*, 95, 574–582.
- Pärtel, M., Kalamees, R., Reier, Ü., Tuvi, E.-L., Roosaluuste, 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.
- Pärtel, M., Mandla, R., & Zobel, M. (1999) Landscape history of a calcareous (alvar) grassland in Hanila, western Estonia, during the last three hundred years. *Landscape Ecology*, 14, 187–196.
- Pautasso, M., & McKinney, M.L. (2007) The Botanist Effect Revisited: Plant Species Richness, County Area, and Human Population Size in the United States. *Conservation Biology*, 21(5), 1333–1340.
- Pilgrim, E.S., Crawley, M.J., & Dolphin, K. (2004) Patterns of rarity in the native British flora. *Biological Conservation*, 120, 165–174.
- Pitman, C.A., Terborgh, J., Silman, M.R., & Nuñez, V. (1999) Tree species distributions in an upper Amazonian forest. *Ecology*, 80, 2651–61.
- Pressey, R.L., & Cowling, R.M. (2001) Reserve Selection Algorithms and the Real World. *Conservation Biology*, 15, 275–277.
- Pressey, R.L., Ferrier, S., Hager, T.C., Woods, C.A., Tully, S.L., & Weinman, K.M. (1996) How well protected are the forests of north-eastern New South Wales? -- Analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. *Forest Ecology and Management*, 85, 311–333.
- Primack, R.B. (1993) *Essentials of conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Pykälä, J. (2000) Mitigating Human Effects on European Biodiversity through Traditional Animal Husbandry. *Conservation Biology*, 14, 705–712.
- Rabinowitz, D. (1981) Seven forms of rarity. Pages 205–217 in H. Synge, editor. *The biological aspects of rare plant conservation*. John Wiley & Sons, New York.
- Rabinowitz, D., Cairns, S., & Dillon, T. (1986) Seven forms of rarity and their frequency in the flora of the British isles. Pages 182–204 in: M.E. Soulé, editor.

- Conservation biology. The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.
- 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 silviculture. *Scandinavian Journal of Forest Research*, 20, 145–152.
- Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., & Yan, X. (2004) Effectiveness of the global protected area network in representing species diversity. *Nature*, 428, 640–643.
- Rodrigues, A.S.L., & Gaston, K.J. (2001) How large do reserve networks need to be? *Ecology Letters*, 4, 602–609.
- Rohlf, D.J. (2006) Key international and U.S. laws governing Management and conservation of biodiversity. Pages 104–108 in: M.J. Groom, G.K. Meffe & C.R. Carroll, editors. *Principles of Conservation Biology*. 3. ed. Sinauer Associates, Sunderland, Massachusetts.
- Roose, A., Sepp, K., Saluveer, E., Kaasik, A., & Oja, T. (2007) Neighbourhood-defined approaches for integrating and designing landscape monitoring in Estonia. *Landscape and Urban Planning*, 79, 177–189.
- Rosenvald, R., & Lõhmus, A. (2008) For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management*, 255, 1–15.
- Rozenzweig, M.L. (2004) Applying Species-Area Relationships to Conservation of Species Diversity. Pages 325–343 in M.V. Lomolino & R.H. Lawrence, editors. *Frontiers of biogeography: New Directions in the Geography of Nature*. Sinauer Associates, Sunderland, Massachusetts.
- Schmidt, T., Arens, P., Smulders, M.J.M., Billeter, R., Liira, L., Augenstein, I., & Durka, W. (in press) Effects of landscape structure on genetic diversity of *Geum urbanum* L. populations in agricultural landscapes. *Flora – Morphology, Distribution, Functional Ecology of Plants*.
- Sætersdal, M., Gjerde, I., & Blom, H.H. (2005) Indicator species and the problem of spatial inconsistency in nestedness patterns. *Biological Conservation*, 122, 305–316.
- Stevens, H.H.M. (2006) Placing local plant species richness in the context of environmental drivers of metacommunity richness. *Journal of Ecology*, 94, 58–65.
- Sutherland, W.J., Pullin, A.S., Dolman, P.M., & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology and Evolution*, 19, 305–308.
- Svenning, J.C., Normand, S., & Skov, F. (2008) Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography*, 31, 316–326.
- Söderström, L. (1992) Invasions and range expansions and contractions of bryophytes. Pages 131–158 in J.W. Bates & A.M. Farmer, editors. *Bryophytes and lichens in a changing environment*. Clarendon Press, Oxford.
- Teder, T., Moora, M., Roosalu, E., Zobel, K., Pärtel, M., Kõljalg, U., & Zobel, M. (2007) Monitoring of biological diversity: a common-ground approach. *Conservation Biology*, 21, 313–317.
- Tilman, D., May, R.M., Lehman, C.L., & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, 371, 65–66.

- Turner, W.R., Wilcove, D.S., & Swain, H.M. (2006) Assessing the Effectiveness of Reserve Acquisition Programs in Protecting Rare and Threatened Species. *Conservation Biology*, 20, 1657–1669.
- Vanderpoorten, A., & Engels, P. (2003) Patterns of bryophyte diversity and rarity at a regional scale. *Biodiversity and Conservation*, 12, 545–553.
- van Diggelen, R., & Marrs, R.H. (2003). Restoring plant communities - introduction. *Applied Vegetation Science*, 6, 106–110.
- Vellak, A., Tuvi, E.-L., Reier, Ü., Kalamees, R., Roosalu, E., Zobel, M., & Pärtel, M. (in press) Past and present effectiveness of protected areas for conservation of naturally and anthropogenically rare plant species. *Conservation Biology*.
- Vellak, K., Kannukene, L., Ingerpuu, N., & Leis, M. (2001) Additions to the list of the Estonian bryophytes, 1997–2001. *Folia Cryptogamica Estonica*, 38, 71–78.
- Vellak, K., Vellak, A., & Ingerpuu, N. (2007) Reasons for moss rarity: Study in three neighbouring countries. *Biological Conservation*, 135, 360–368.
- WallisDeVries, M.F., Poschlod, P., Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, 104, 265–73.
- White, E.P., Adler, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., Kaufman, D.M., Rassweiler, A., Rusak, J.A., Smith, M.D., Steinbeck, J.R., Waide, R.B., & Yao, J. (2006) A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos*, 112, 185–195.
- Wiklund, K. (2002) Substratum preference, spore output and temporal variation in sporophyte production of the epixylic moss *Buxbaumia viridis*. *Journal of Bryology*, 24, 187–195.
- Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M.R., & Possingham, H.P. (2007) Conserving Biodiversity Efficiently: What to Do, Where, and When. *PLoS Biology*, 5, 223.
- Witte, J.-P.M., & Torfs, J.J.F. (2003) Scale dependency and fractal dimension of rarity. *Ecography*, 26, 60–68.
- Wood, B. (2001) Maintaining vegetation diversity on reserves: the relationship between persistence and species richness. *Biological Conservation*, 97, 199–205.
- Zechmeister, H.G., Tribsch, A., Moser, D., Peterseil, J., & Wrška, T. (2003) Biodiversity ‘hot spots’ for bryophytes in landscapes dominated by agriculture in Austria. *Agriculture, Ecosystems & Environment*, 94, 159–167.
- Zar, J.H. (1996) Biostatistical analysis. Prentice-Hall, London.
- Zobel, M., & Pärtel, M. (2008) What determines the relationship between plant diversity and habitat productivity? *Global Ecology and Biogeography*, 17, 679–684.

SUMMARY IN ESTONIAN

Ruumilis-ajalised aspektid taimeliikide kaitstes

Bioloogilise mitmekesisuse e. biodiversiteedi kaitse kontseptsioon moodustab keskse osa looduskaitsebioloogias. Väärtused, mida kannab endas biodiversiteet, on leidnud arvestatava koha ühiskondlikus mõtlemises ning majanduslikus tegevuses. Sellest tulenevalt lisandub bioloogilise mitmekesisuse biootilisele olemusele ka filosoofiline, sotsiaalne, kultuuriline ning ökonoomiline aspekt. Kogu sellise integreerituse juures jääb oluliseks siiski traditsiooniline looduskaitseline lähenemisviis, kus erinevate looduskaitsevõtetega üritatakse tagada bioloogilise mitmekesisuse säilimine.

Bioloogilise mitmekesisuse mitmetahuline olemus, alates molekulaarsest tasandist ning lõpetades ökosüsteemide tasandiga, sunnib käsitlema sellega seotud teemasid teatud lihtsustustega ning üldistavate mudelite kasutamisega. Looduskaitsebioloogia erinevate kontseptuaalsete lähenemisviiside, näiteks „liigirikkuse tulipunktid”, saarte teooria jne juures on jätkuvalt päevakorras traditsioonilised käsitlused nagu ohustatud ning haruldased liigid ja looduskaitsealad. Liigitasandil tehtavad uuringud jäävad kergemini hoomatavamaks ning arusaadavamaks ka laiemale ringkonnale kui vaid looduskaitsebioloogid, hoolimata liigikontseptsiooni teatud määramatusest ning liikide defineerimise keerukusest.

Looduskaitse ülesanded liigitasandil muutuvad komplitseeritumaks kui lisanduvad liikide erinevad jaotused ruumi- ning ajaskaalal. Liikide mitmekesisuse muutmise tekkimise seaduspärasuste selgitamine ning ajaliste muutuste prognoosimine on olulise tähtsusega looduskaitse teoorias ja praktikas. Teadmine, et kõik taimeliigid ei ole võrdse olulisusega kaitse organiseerimise osas, nõuab selgepiirilist liikide kategoriseerimist ja prioritseerimist looduskaitse ülesannete optimaalseks lahendamiseks. Ajalis-ruumilisi aspekte liigikaitstes aitab hinnata liikide jaotumine looduskaitsealade lõikes. Samaaegselt võimaldab haruldaste liikide kaitse kaitsealadel hinnata ka kaitsealade süsteemi enda efektiivsust, täielikkust jne. Liikide kaitse organiseerimise muudab keerukamaks erinevate taksonoomiliste rühmade kooskäsitlemine. Näiteks haruldaste soontaimede ja sammalde erinev ruumiline jaotus viitab selgelt vajadusele erinevateks käsitlusteks erinevates taksonoomilistes üksustes.

Haruldased taimeliigid võib jagada kahte suurde gruppi – looduslikult haruldased ning inimtegevusest põhjustatud häiritust vajavad liigid. Esimese grupi moodustavad liigid, millel on vähe kasvukohti, väike levikuulatus, populatsioonis vähe isendeid või sõltuvad mingist spetsiifilisest substraadist. Teise grupi kuuluvad liigid, mis vajavad teatud häiringuid, näiteks väikese intensiivsusega põllumajanduslikke või metsamajanduslikke tegevusi. Liikide looduskaitse staatus fikseeritakse tihtipeale mitmesugustes seadusandlikes aktides või ühiskondlikes kokkulepetes nn Punaste Raamatute nimekirjades erinevatel skaaladel: ülemaailmne, regionaalne, riiklik. Nendes nimekirjades esitatud liikide harulduse aste on olulises sõltuvuses hindamiskriteeriumitest,

piirkonna suurusest ning arenguloost. Haruldasi liike võib leida väikesepindalises riigis rohkem kui suurepindalises riigis, sest näiteks väiksemal territooriumil võib olla oma levila piiril olevate taimeliikide leiukohti lihtsalt vähem. Seega võib tekkida olukord, kus väikeriigi looduskaitsestandardid võivad olla oluliselt rangemad kui mõnes suurriigis.

Looduskaitstes on leidnud oma teoreetilis-rakendusliku koha haruldaste liikide lähenemisviisi kõrval ka looduskaitsealad ning neist moodustuvad võrgustikud. Looduskaitsealade ja liikide kaitse puhul on sätestatud mitmesuguseid kvantitatiivseid standardeid, et määrata, kas looduskaitseline tegevus kulgeb soovitud suunas. Ülemaailmne Looduskaitseorganisatsioon (IUCN) on kehtestanud normi, et igas riigis peaks olema looduskaitsealadega kaetud 10%. Taimeliikide kaitse strateegia sätestab, et vähemalt 60% haruldastest taimeliikidest peab olema kaitstud *in situ* st enamusjaolt erinevat tüüpi kaitsealadel ning 50% taimeliikide kõrge mitmekesisusega aladest peab olema kaitse all aastaks 2010. Uuringud on näidanud, et sellised kvantitatiivsed näitajad võivad jääda liiga kergelt saavutatavaks kui kasutatakse lihtsakoelisi hindamismeetodeid. Ainuüksi erinevate taksonoomiliste rühmade ning looduskaitsealadest erinevate gruppide samaaegne kasutamine muudab sisulist tähendust neil kvantitatiivseil standarditel.

Bioloogilise mitmekesisuse levimise ruumiliste seaduspärasuste kõrval jääb oluliseks määrata ka muutuste ajaline erinevus. Mitmed looduskaitsealad kontseptsioonid – liigifond, väljasuremisvõlg, koosluste suksessioonid, maastike heterogeensus jne – sisaldavad olulisel määral ajalisi aspekte. Ka looduskaitse kaitsekorralduslik tegevus ise on ajaliselt muutuv. Kaitsealade võrgustiku vajakute analüüs on laialt levinud ruumilise analüüsi mõttes, kuid analoogset tegevust on vaja korraldada ka ajalises skaalas.

Integreeritud lähenemine, kuhu on kaasatud haruldased, ohustatud ning kaitsealused liigid ja looduskaitsealad ning kus analüüsis arvestatakse ruumilisi ning ajalisi mõjusid, suudab tagada erinevate kvantitatiivsete ja kvalitatiivsete näitajate olemuse mõistmise ning eesmärkide saavutamise. Nende aspektide uurimisele keskendubki käesolev töö.

Töö eesmärkideks oli uurida:

1. kuidas arendada liikide kategoriseerimise ja prioritseerimise süsteemi, mis hõlmaks taimeliikide nii looduslikku kui ka inimõigulist haruldust.
2. kas erinevate looduskaitsealade vajadustega soontaimed vajavad erinevat arvu kaitsealasid ning kas kaitset vajavate soontaimede grupid on olnud kaetud kaitsealadega ühtlaselt läbi ajaloo.
3. kas regionaalsel tasemel haruldaste samblaliikide harulduse põhjuseks on nende ökoloogilised nõudlused, substraadispetsiifilisus, elustrateegia või on nad taksonoomiliselt haruldased.

Eesmärkide saavutamiseks grupeerisime ja prioritseerisime Eesti soontaimed kaheksasse gruppi, millest neli olid moodustatud loodusliku harulduse baasil (piiratud globaalne levik, piiratud lokaalne levik, haruldane kasvukoht, alati väike populatsioon) ning neli inimõigulise harulduse alusel (rohumaade

niitmine, väikese intensiivsusega häiring, ekstensiivne põllumajandus, korjamise oht). Andmetöötluses on kasutatud peakomponentanalüüsi, kasutades kaheksat faktorit ning 301 taimeliiki. Looduskaitsealade kaitsekorraldusliku efektiivsuse hindamiseks kasutasime 289 taimeliiki 301-st, 33 looduskaitseala ning liikide akumulatsioonikõveraid.

Sammalde harulduse põhjuste hindamiseks kasutasime kolme Balti riigi sammalde liiginimestikke, mille alusel koostati erinevate esinemissagedusega liikide grupid. Neist gruppidest valiti 184 kontrastse sagedusega liiki kolmes erinevas grupis: 1) sagedased liigid, esinedes kõikides Balti riikides; 2) haruldased liigid, esinedes kõikides Balti riikides; ning 3) väga haruldased liigid, esinedes vaid ühes Balti riigis.

Töö tulemusel selgus, et erinevad looduskaitsealad olid kaetud erineva arvu soontaimeliikidega. Liikidega hõlmatud oli järgmine: piiratud globaalne levik 38%, piiratud lokaalne levik 28%, rohumaade niitmine 32%, korjamise oht 31% alati väike populatsioon 21%. Kõige vähem oli liike haruldaste kasvukohtade grupis 7%. Väikese intensiivsusega häiringu ning ekstensiivne põllumajanduse grupis oli mõlemas 10% liike (Tabel 1).

Looduskaitsealad katsid erinevate kaitseväärtusega soontaimede liikide gruppe erinevalt. Et oleks tagatud looduskaitsealade eesmärkide täitmine – 60% haruldastest liikidest oleks kaitstud – vajavad looduslikult haruldaste liikide grupid kaks korda enam kaitsealasid kui inimõiguliselt haruldaste liikide grupid. Erilist tähelepanu peaksid väärima liigid, mis on piiratud lokaalse levikuga või mis vajavad spetsiifilist kasvukohta. Akumulatsioonikõveraid üksikult võttes võib mõni haruldusegrupp saada põhjendamatult suurema tähelepanu (Joonis 1). Kaitsealade moodustamist ning liikide kaitset ajaskaalas vaadates selgus, et haruldaste leivukohtadega liigid olid olnud suurema tähelepanu all kui ülejäänud. Inimõiguliselt haruldasi liike, mis olid seotud ekstensiivse põllumajandusega, ei olnud üldse tähelepanu saanud (Joonis 2g).

Analüüsides erineva esinemissagedusega samblaliike Baltimaades selgus, et sammalde haruldusastme määravad eelkõige ökoloogilised ja elustrateegia parameetrid, vaheseimal määral on harulduse põhjused määratud ka kasvukohanõudluste ja taksonoomiliste eripärasuste poolt.

Töö tulemused viitavad asjaolule, et looduskaitsealade tegevuste planeerimisel on vajalik rakendada erinevaid võtteid ning lähenemisi, et tagada looduskaitsealade eesmärkide sisuline saavutamine. Ruumiliste ja ajaliste skaalade ning taksonoomiliste üksuste erinevus võib anda erinevaid tulemusi otsustuste tegemiseks. Haruldaste liikide ja kaitsealade kontseptsioonid on leidnud laialdase tunnustuse looduskaitsealade tegevuste planeerimisel. Sellest hoolimata peab kontseptsioonide raames kasutatavaid meetodeid ning tulemuste interpretatsioone täiendama. Traditsioonilised lähenemisviisid, kus algselt eristatakse haruldased liigid, nende ruumiline jaotus ning selle alusel korraldatakse kaitset kas kaitsealade moodustamise kujul või kaitsealade liikide nimekirjade kehtestamisega, on taganud seni teatud edu. Ümbritsevas keskkonnas toimivate protsesside keerukus sunnib aga käsitlema looduskaitsealade probleeme laiemas kontekstis. Ainuüksi inimtegevuse iseloomu muutus kas

oma intensiivsuses või laienemises on põhjustanud liikide haruldusastmete muutusi. See omakorda nõuab kaitsekorralduslike tegevuste kohandamist vastavalt uutele tingimustele. Ilmselgelt hakkab ülekaalu saavutama aktiivne kaitsekorraldus passiivse üle. Üha rohkem on haruldaste taimeliikide kaitstes vaja ka otsest inimtegevuse sekkumist, näiteks traditsiooniliste majandustegevuste jätkamist. Vastavalt Eesti asustuse arenguloole on mitmed kooslused looduslike asemel kujunenud juba poollooduslikeks ning siin levivad haruldased liigid vajavad pikaajaliseks eksisteerimiseks inimtegevuse abi. Mõnikord vajab taimeliigi harulduse mõtestamine kardinaalset muutust suhtumises harulastesse taimeliikidesse. Traditsiooniliste, ekstensiivsele põllumajandusele vastavate, umbrohtude arvamine haruldaste liikide hulka tundub looduskaitsealiselt väheviljakas tegevus olevat, bioloogilise mitmekesisuse säilitamise kontseptsiooni kohaselt aga mitte.

Looduskaitseliste strateegiatega kvantifitseeritud eesmärgid (näit. 10% riigi territooriumist peab olema kaitsealadega kaitstud, jne) suudavad pakkuda pealtnäha kergesti mõistetavaid kriteeriume. Lähemal analüüsimisel aga selgub, et need kriteeriumid „ei tööta” alati päris hästi. Teatud juhtudel on võimalik vastavad normid väga kiiresti täita. Sisukal analüüsil ilmneb, et hoolimata numbrilisest saavutusest jääb looduskaitsealine sisuline eesmärk ise täitmata. Liikide ja kaitsealade akumulatsioonikõverate laiad usalduspiirid viitavad määramatusel üksiknumbrite interpreteerimisel. Ülemine usalduspiir viitab võimalusele, et hoolikal kaitsealade valikul on võimalik saavutada 60% haruldaste taimeliikide kaitstus ka väheste kaitsealade olemasolul. Tegelikult määrab selle võimaluse hoopis asjaolu, kas juhuslikult valitud kaitsealad asuvad liigirikastes piirkondades või mitte. Sageli paiknevad kaitsealad pigem vähematraktiivsetes piirkondades. Seega peaksime kasutama hinnangute andmisel hoopis alumist usalduspiiri. Sellest tuleneb konkreetne praktiline lahendus, et tagada näiteks liikide 85% kaitstus kaitsealadega, peame suurendama väga kiiresti kaitsealade arvu.

Analüüsides haruldaste taimeliikide kaitstust kaitsealade poolt ajalisel skaalal tõi välja samuti erinevused haruldaste taimeliikide gruppide vahel. Kaitsealade asutamine erinevatel perioodidel näitab, et looduslikult haruldasi taimeliike on eelistatud oluliselt enam kui inimõju häiringuid vajavaid grappe. Alles viimasel ajal on seoses erinevate poollooduslike koosluste väärtustamisega tähelepanu alla võetud ka inimõju vajavad haruldased liigid. Looduskaitset väärivate liikide grupeerimine ja prioritseerimine võimaldab pöörata tähelepanu üheaegselt laiemale hulgale taimeliikidele selle asemel, et keskenduda üksikutele liikidele. Näiteks, kaitsekorralduslikult on võimalik teha järeldusi, et haruldased taimeliigid, mis vajavad koosluse niitmist, ei nõua sealjuures otseselt kaitsekorraldust eraldi iga üksiku liigi tasemel.

Sammalde puhul saab harulduse põhjustest kõnelda eelkõige ökoloogiliste parameetrite ja elustrateegiast tuleneva alusel. Haruldased samblaliigid Balti riikide lõikes on seotud substraadi aluselise ja aasta keskmise temperatuuriga. Haruldaste samblaliikide arv kahaneb põhjast lõuna suunas, olles kõige

madalam Leedus, kus aluselist substraati esineb kõige vähem, kuid aasta keskmised temperatuurid on kõrgemad.

Kokkuvõtvalt saab väita, et looduskaitse süstemaatiline planeerimine vajab otsuseid, milles on arvestatud nii ruumilisi kui ka ajalisi aspekte ning erinevaid taksonoomilisi rühmi. Looduskaitsest mõjusamaid üldistusi võimaldavad teha looduskaitsest väärtust omavate taimeliikide grupeerimine ja prioritiiseerimine. Kaitset väärivate liikide grupid on efektiivne võimalus kaitsekorralduslike tegevuste paremaks planeerimiseks praktikas. Taimeliikide grupeerimine vastavalt looduskaitsele väärtustele omab üldisemat tähendust kui ainult riiklikul või regionaalsel tasandil tehtud rakendustes. Integreerides liikide kategoriseerimise ja prioritiiseerimise tulemused ning looduskaitsealade kontspetsioonid, on võimalik hinnata kaitsealade võrgustiku efektiivsust erinevate aspektide alusel. Liikide akumulatsioonikõverate meetodi kasutamine võimaldab teha olulisi järeldusi ka praktilisele looduskaitsele, kuna näitab, et liikide haruldusegrupid ei ole ühtlaselt kaitsealade poolt kaitstud, looduskaitse huvid on sajandi jooksul olnud gruppide lõikes erinevad ning erinevad grupid võivad käituda üldiste looduskaitsest kvantitatiivsete eesmärkide suhtes erinevalt.

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PUBLICATIONS

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Publications

Articles indexed by ISI Web of Science

Pärtel, M., Kalamees, R., Reier, Ü., Tuvi, E-L., Roosalu, 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

Vellak, K., Vellak, A., Ingerpuu, N. (2007) Reasons for moss rarity: study in three neighbouring countries. *Biological Conservation*, 135, 360–368

Vellak, A. Tuvi E-L, Reier Ü, Kalamees R, Roosalu E. Zobel M, Pärtel M. (in press) Past and Present Effectiveness of Protected Areas for Conservation of Naturally and Anthropogenically Rare Plant Species. *Conservation Biology*.

Conference thesis

Vellak, K., Vellak, A., Ingerpuu, N. “Do existing protected areas guarantee persistence of bryological diversity in Estonia? Conference “Bryophyte conservation, status and perspectives”. Cluj-Napoca, September 2007, Romania.

Vellak, A., Vellak, K., Pärtel, M. How well protected areas cover plant diversity: a national scale study. 1-st European Congress of Conservation Biology “Diversity for Europe”. Eger, August 2006, Hungary.

Vellak, K., Vellak, A., Ingerpuu, N. „Reasons for moss rarity in the Baltic States”, konverents „Conservation Ecology of Cryptogams”. Bispgården, November 2005, Sweden.

Vellak, A. Conservation genetic resources of plants: botanical garden opportunities. Baltic Botanic Gardens in 2002–2003 Estonia, Latvia, Lithuania. Tartu, p. 61.

Ingerpuu, N., Vellak, A., Vellak, K., Möls, T. „Trends in moss (Bryopsida) diversity“ World Conference of Bryology . Kuala Lumpur, August 2007, Malaysia.

Popular science articles

Tõnisson, A., Vellak, A. (2003) Uusi uurimisandmeid liivakivipaljanditest. *Looduskaitsealaseid töid* 7, 79–88.

Tõnisson, A., Vellak, A. (2006) Vaabinas varises vanakurja varikatus. *Eesti Loodus*, 6, 22–24.

Grants and scholarships:

Senior personnel in grant:

ETF6614 (Meelis Pärtel) Macroecological processes determining plant community diversity and function

2006, 2008 Traveling grants, Doctoral School of Ecology and Environmental Sciences.

Other scientific activities:

Membership in societies:

Rõuge Energy Centre

Haanja Nature Park Council

ELULOOKIRJELDUS

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Jõgeva-Tartu regioon

Haridus

1995–1998 Tartu Ülikool, teadusmagistri kraad maastikuökoloogias ja
keskkonnakaitstes. "Eesti kaitsealade süsteem:
ruumiline analüüs."
1982–1986 Tartu Riiklik Ülikool
1980–1982 Võru 1. Keskkool

Keelte oskus: eesti, inglise, vene

Töökogemus

alates 2009 kaitseplaneerimise spetsialist, Keskkonnaamet,
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2006–2009 seire ja teadustöö spetsialist, Riiklik Looduskaitsekeskus
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Peamised uurimisvaldkonnad: looduskaitsebioloogia, kaitsealade ruumiline
paiknemine

Publikatsioonide loetelu

Artiklid, mis on kajastatud ISI Web of Science andmebaasis

Pärtel, M., Kalamees, R., Reier, Ü., Tuvi, E-L., Roosalu, 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

Vellak, K., Vellak, A., Ingerpuu, N. (2007) Reasons for moss rarity: study in three neighbouring countries. *Biological Conservation*, 135, 360–368

Vellak, A. Tuvi E-L, Reier Ü, Kalamees R, Roosalu E. Zobel M, Pärtel M. (in press) Past and Present Effectiveness of Protected Areas for Conservation of Naturally and Anthropogenically Rare Plant Species. *Conservation Biology*.

Konverentside ettekanded

Vellak, K., Vellak, A., Ingerpuu, N. “Do existing protected areas guarantee persistence of bryological diversity in Estonia? Konverents “Bryophyte conservation, status and perspectives” Cluj-Napoca, September 2007, Rumeenia.

Vellak, A., Vellak, K., Pärtel, M. How well protected areas cover plant diversity: a national scale study. 1-st European Congress of Conservation Biology “Diversity for Europe” Eger, August 2006, Ungari.

Vellak, K., Vellak, A., Ingerpuu, N. „Reasons for moss rarity in the Baltic States”, konverents „Conservation Ecology of Cryptogams”, Bispargen, November 2005, Rootsi.

Vellak, A. Conservation genetic resources of plants: botanical garden opportunities. Baltic Botanic Gardens in 2002–2003 Estonia, Latvia, Lithuania. 2004, Tartu, lk. 61.

Ingerpuu, N., Vellak, A., Vellak, K., Möls, T. „Trends in moss (Bryopsida) diversity” World Conference of Bryology Kuala Lumpur, August 2007, Malaysia.

Populaarteaduslikud artiklid

Tõnisson, A., Vellak, A. (2003) Uusi uurimisandmeid liivakivipaljanditest. *Looduskaitsealaseid töid* 7, 79–88.

Tõnisson, A., Vellak, A. (2006) Vaabina varises vanakurja varikatus. *Eesti Loodus*, 6, 22–24.

Saadud uurimistoetused ja stipendiumid

Põhitäitja grandis:

ETF6614 (Meelis Pärtel) Makroökoloogilised protsessid taimekoosluse mitmekesisuse ja talitluse määratlejana.

2006, 2008 Ökoloogia ja keskkonnateaduste doktorikooli reisistipendium

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