GLOBALLY WIDESPREAD BRYOPHYTES, BUT RARE IN EUROPE

Tomas Hallingbäck

Swedish Threatened Species Unit, P.O. Box 7007, SE-75007 Uppsala, Sweden.
Tomas.Hallingback@dha.slu.se

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The need to save not only globally threatened species, but also regionally rare and declining species in Europe is discussed. One rationale of red-listing species regionally is to be preventive and to counteract the local species extinction process. There is also a value in conserving populations at the edge of their geographical range and this is discussed in terms of genetic variation. Another reason is the political willingness of acting locally rather than globally. Among the rare and non-endemic species in Europe, some are rare and threatened both in Europe and elsewhere, others are more common outside Europe and a third group is locally common within Europe but rare in the major part. How much conservation effort should be put on these three European non-endemic species groups is briefly discussed, as well as why bryophytes are threatened. A discussion is given, for example, of how a smaller total distribution range, decreasing density of localities, smaller sites, less substrate and lower habitat quality affect the survival of sensitive species. This is also compared with species that have either high or low dispersal capacity or different longevity of either vegetative parts or spores. Examples from Sweden are given.

Key words: Bryophytes, rarity, Europe, dispersal capacity, Sweden.

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É discutida a necessidade de preservar na Europa não só globalmente as espécies ameaçadas, mas também regional-mente as espécies raras ou em declínio. Uma lista vermelha racional de nível regional deve ser preventiva e contrariar o processo da extinção local de determinada espécie. Uma outra

razão é a vontade política de actuar mais a nível regional que global. Entre as espécies consideradas raras mas não endémicas da Europa, algumas são raras ou ameaçadas quer a nível europeu quer no geral, outras são mais frequentes fora da Europa e, num terceiro grupo podem ser regionalmente comuns na Europa mas raras na maior parte da sua área geral. Neste sentido é apresentado o que se deve investir na conservação destes três grupos de espécies e a causa da sua ameaça. É discutido ainda como poderá sobreviver uma espécie sensível que apresente uma distribuição restrita, com decréscimo na densidade de locais, locais restritos, pequena amplitude de substratos e baixa qualidade de habitats. Esta situação é comparada com a de espécies que apresentam alta ou baixa capacidade de dispersão, ou diferentes longevidades, quer nas estruturas vegetativas quer nos esporos. São apresentados vários exemplos de espécies existentes na Suécia.

Palavras chave: Briófitos, raridade, Europa, capacidade de dispersão, Suécia.

INTRODUCTION

Alteration, fragmentation and, finally, loss of natural habitats, are major causes of the increasingly rapid decline in the overall biotic diversity on Earth. Usually the effects are measured as globally threatened or irreversible loss of species. For the regionally vanishing populations the processes, however, may have started long before any of the individual species actually disappear.

Among all rare and non-endemic species in Europe, some are rare both in Europe and elsewhere, e.g. *Distichophyllum carinatum* Dixon & Nicholson (fig. 1) and *Jamesoniella undulifolia* (Nees) K. Müll. A second group encompasses species that are widespread outside Europe, e.g. *Anacamptodon splachnoides* (Froelich ex Bridel) Bridel, *Bryhnia novae-angliae* (Sull. & Lesq.) Grout (fig. 2)*, Dicranum viride* (Sull. & Lesq.) Lindb., and *Sphagnum angermanicum* Melin, which are rare in Europe but widespread and locally common in some areas of eastern North America. Other rare European species are common in Africa, Asia or Australia. A third group is made up of those that are rare or common outside Europe, but that within Europe have an uneven distribution pattern and may even be locally common in a small part of Europe but rare in the major part, e.g., *Buxbaumia viridis* (Lam. & DC.) Moug. & Nestl. (fig. 3), *Eurhynchium pumilum* (Wils.) Schimp. and *Pseudo-calliergon turgescens* (T. Jens.) Loeske.

The question is how much conservation effort should be put on these three European non-endemic species groups.

First, the different reasons why some species are rare or declining locally, regionally or globally, and what factors are increasing their extinction risk.
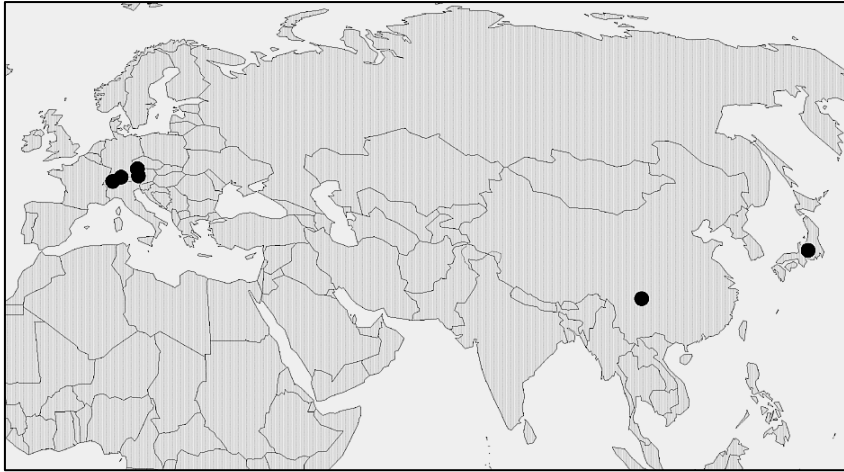
Figure 1. Known world distribution of *Distichophyllum carinatum* Dixon & Nicholson. Sources to the map: Austria (GRIMS 1999); China (Z. Iwatsuki *pers. comm.*); Germany (R. Lübenau-Nestle *pers. comm.* 1998); Japan (Z. Iwatsuki *pers. comm.*); Switzerland (E. Urmi *pers. comm.* 2000).
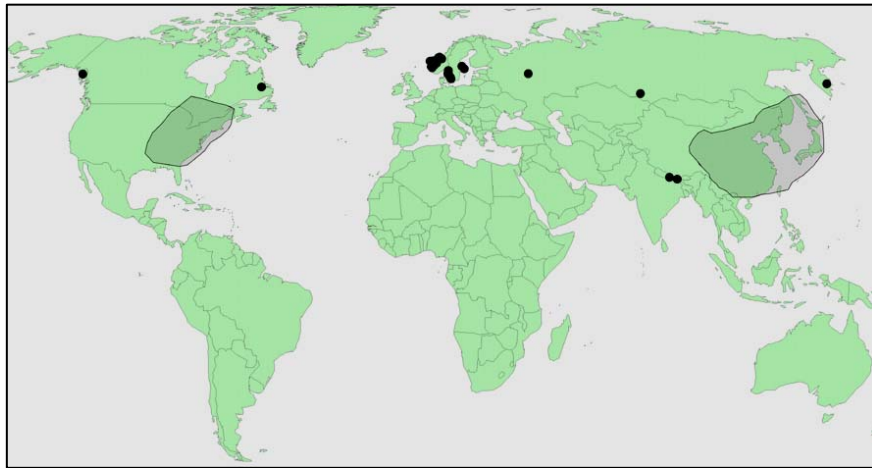

Figure 2. Known world distribution of *Bryhnia novae-angliae* (Sull. & Lesq.) Grout. Sources to the map: BOHLIN *et al.* 1981, with additions received from M. Ignatov and Z. Iwatsuki *pers. comm.* 2001.
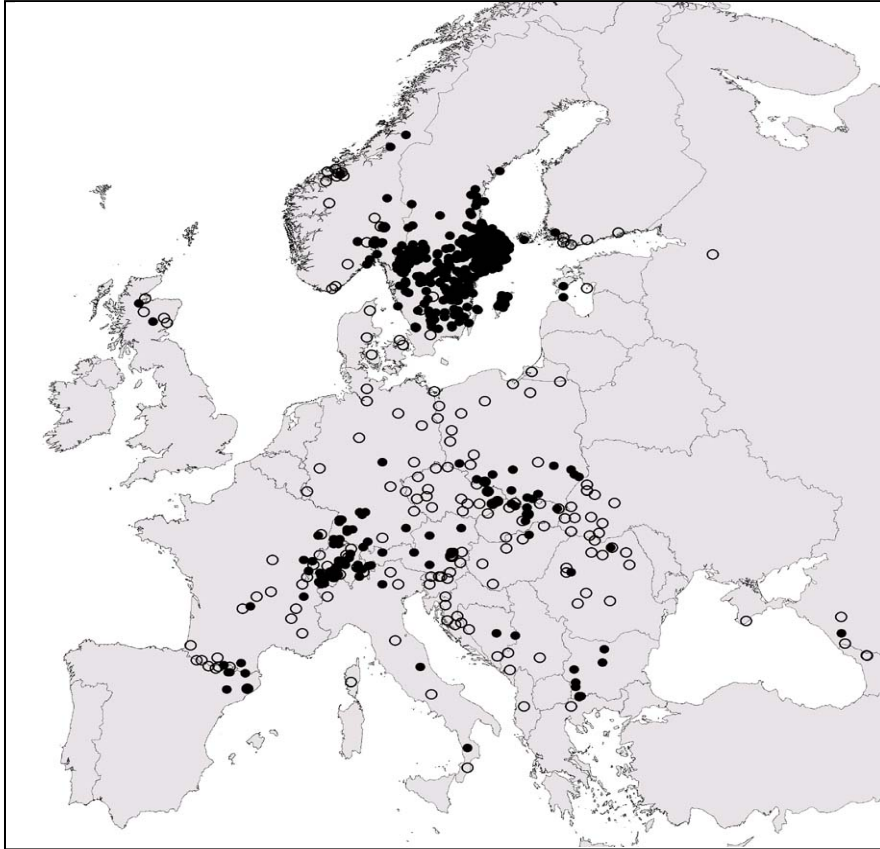
Figure 3. Known European distribution of *Buxbaumia viridis* (Lam. & DC.) Moug. & Nestl. Open circle = finding before 1980; Black dots = finding after 1979. Sources to the map: Austria (GRIMS 1999); Balcan region (M. Sabovljevic *pers comm.* 1998 & SABOVLJEVIC *et al.* 1999); Britain (N. Hodgetts *pers. comm.*1999); Bulgaria (A. Ganeva *pers. comm.* 1998); The Czech Republic (J. Váňa *pers. comm.* 2001); Denmark (JENSEN 1959); Estonia (N. Ingerpuu *pers. comm.* 1998); Finland (LAAKA & SYRJÄNEN 1990); France and Belgium (R. Schumacker & J. Sapaly *pers. comm.*); Germany (DÜLL & MEINUNGER 1989); Hungary (B. Papp *pers. comm.* 1998); Italy (M. Aleffi *pers. comm.*1998 and CASTALDO 1973); Kaliningrad (DIETZOW, 1938); Luxembourg (J. Werner *pers. comm.* 1998); Norway (HASSEL & GAARDER 1999); Poland (SZMAJDA *et al.* 1991); West Russia (M. Ignatov & O. Afonina *pers. comm.* 2001); Slovakia (R. Soltes *et al. pers. comm.* 1998); Spain (M. Brugués *pers. comm.* 1998, INFANTE & HERAS 2001); Sweden: (HALLINGBÄCK 1998); Switzerland (E. Urmi *pers. comm.* 2001).

FACTORS AFFECTING EXTINCTION RISK OF BRYOPHYTES

The first process I would like to discuss is the gradual loss of suitable habitats and degradation of habitat quality and how much that affects the status of rare and vulnerable bryophytes. What does a smaller total distribution range mean for the survival of different species? What does the combination of increased isolation of subpopulations and low reproductive capacity imply in terms of population dynamics as well as inbreeding and loss of intraspecific variation?

How can decreasing density of localities lead to extinction?

The decline of a population can be observed as a decrease in density of localities within a distribution range. In south Sweden, for example, the area of natural peat-lands and fens has become reduced and fragmented during the last millennium. The number of localities for *Hamatocaulis vernicosus* (Mitt.) Hedenäs and *Meesia longiseta* Hedw. is today less than half of these fifty years ago in two provinces of South Sweden (HALLINGBÄCK 1998). Deforestation and juvenilization of forests has resulted in reduction of suitable habitats for epiphytic species such as the mosses *Neckera pennata* Hedw. and *Dicranum viride* (Sull. & Lesq.) Lindb. *Neckera pennata* has been classified as a satellite species, i.e. a species with small populations in only a few of the available localities (KUUSINEN & PENTTINEN 1999). According to SÖDERSTRÖM & JONSSON (1992), a satellite species has a high probability of becoming extinct.

Old-growth spruce forests with decaying logs are rapidly decreasing in north Europe and the remaining stands are scattered and often well separated. For example, the liverwort, *Lophozia longiflora* (Nees.) Schiffn., is restricted to decaying logs and its distribution range has been reduced due to changes in forest practice. According to forestry statistics, the area of old-growth forest in central and northern Sweden has decreased from 766 000 ha in the period 1983–87 to 680 000 in 1989-93 outside protected areas (ANONYMOUS 1997). This is a decline of 11% in 6 years and this trend seems to continue. Most epixylic species are generally adversely affected (SÖDERSTRÖM 1988) and many are rare and decreasing. That may depend on the shortage of habitats and on site isolation. The extinction risks increase due to decreasing substrate availability with increased fragmentation in distribution and smaller populations. In addition, successful diaspore dispersal becomes less, due to a smaller population, lower diaspore production and increased distances to cross (SÖDERSTRÖM 1992).

Some habitats have always been naturally patchy, e.g. islands and mountains, and taxa confined to these habitats may be well adapted to this situation, and what it implies in terms of isolation, increased environmental stress, edge effects, etc. On a small-scale, animal dung provides another example of a naturally fragmented habitat. However, according to hunting and agricultural practices such habitats increase or decrease. Species of such habitats have evolved dispersal mechanisms to cope with fragmentation, i.e. insect-dispersal for dung species and wind-dispersal for other fugative species adapted to fragmented

substrates. A third example is the short-lived *Ricciocarpos natans* (L.) Corda, which probably is dispersed by water birds and thus inhabits bird-rich wetlands.

Patchy distribution of small, scattered habitats may lead to extreme rarity, as with bryophytes restricted to copper-rich substrates, e.g. *Scopelophila cataractae* (Mitten) Broth. Long-distance dispersal has probably played an important role in the geographic history of *S. cataractae* (SHAW 1995). Since it occurs predominantly on copper ore, the species has declined in the past as its habitats have been mined and quarried almost to vanishing point in many areas.

In conservation biology, information on the effects of isolation on bryophyte subpopulations is more or less lacking. However, in general, those taxa with a large production of small diaspores are considered to be less affected by isolation (cf. SÖDERSTRÖM & HERBEN 1997) and hence not so vulnerable to isolation through fragmentation of their habitats. Species that produce large diaspores (e.g. *Riccia* spp.) or none or very few, have poor chances of long distance dispersal. The subpopulations may be considered as becoming more easily isolated if the population becomes fragmented compared with species with spore dispersal and good long distance dispersal capacity.

How can low dispersal capacity lead to extinction?

For some species successful long-range dispersal is very rare, or occurs randomly and probably in reality has little significance for breaking or reducing isolation. Ten kilometres between locations may represent total isolation, 50 km between populations of a species without spore dispersal may indicate severe fragmentation, while the corresponding distance for species with spores is 100-1000 km, shorter for species with low production and large spores and longer for those with high production and small spores. It is always critical whether male and female spores from a bisexual source area are able to disperse to sites several kilometres apart, and survive. The two new establishments would, of necessity, be two individuals able to propagate only by vegetative cloning. Such clones could, effectively, be kept apart forever. Only if the species in question is able to produce easily-dispersed propagules can there be an 'escape' from this dilemma. In that case, propagules from a male plant, or from a female plant, could be wind-carried to the perimeter of the clone of the opposite sex. In effect, the two gametangial types are then capable of sexual reproduction. Maximum moss fertilisation ranges seem to be less than 10 cm (LONGTON & SCHUSTER 1983).

Evidence suggests that sexual reproduction is rare in many bryophyte taxa (cf. LONGTON 1992, LONGTON & HEDDERSON 2000). Thus, many taxa, especially dioicous species (LONGTON & SCHUSTER 1983), rarely or never produce sporophytes. Examples of dioicous taxa in Sweden that are rare and threatened are *Bryhnia novae-angliae, Hamatocaulis vernicosus* (Mitt.) Hedenäs*, Loeskeobryum brevirostre* (Brid.) Broth.*, Lophozia laxa* (Lindb.) Grolle*, Porella arboris-vitae* (With.) Grolle*, Scapania degenii* K. Müll.*, Sphagnum angermanicum*

Melin*, Tortula virescens* (De Not.) De Not. and *Trichocolea tomentella* (Ehrh.) Dum.

If spores are rare or lacking, the ability to disperse is limited. Species that rarely produce spores usually instead produce specialised vegetative propagules (LONGTON & SCHUSTER 1983). However, vegetative diaspores are generally considered to be of importance only in short distance dispersal (LONGTON & SCHUSTER 1983).

The significance of asexual bodies, produced by gametophytes, in the survival strategy of dioicous taxa is enormous (LONGTON & SCHUSTER 1983, LONGTON 1992). An example of this in Sweden is the moss *Dicranum viride* that, in this region, only occurs on trunks of deciduous trees and is confined to South Sweden and known from about 10 very small sites. The species is not found with sporophytes in Sweden. However, sporophytes were found in 1868 in South Finland, although today the species is considered extinct in Finland (ENROTH 1989). The leaves are fragile and the broken tips facilitate asexual propagation. The main threats seem to be the very small population size itself and negative impact of air pollution.

Are the species dispersed over long distance safe?

It is clear that bryophytes have a very high potential capacity for dispersal if spores are produced. Theoretically, spores could easily be dispersed by wind over thousands of kilometres (van ZANTEN 1978, van ZANTEN & POCS 1981). CRUM (1972) suggested that spores in the size range 8–12 µm diameter are capable of being carried at least 19,000 km in a moderate wind, although for a spore 28 µm in diameter the theoretical distance is only 320 km. Some evidence for long-range dispersal of bryophytes has been found in the floras of geologically recent, isolated oceanic islands such as Hawaii (SCHOFIELD & CRUM 1972). The size and number of spores is apparently extremely crucial for their ability to establish and colonise new sites. Examples of long-distance dispersed species can be found especially among those with both a colonist strategy and very small and light spores, for example *Aloina rigida* (Hedw.) Limpr. (15 µm), *Aongstroemia longipes* (Somm.) Bruch & Schimp. (16 µm) and *Buxbaumia viridis* (Lam. & DC.) Moug. & Nestl. (12 µm). However, for spore-dispersed taxa the risk of extinction may instead be the lack of suitable substrate or habitat.

Can a severely fragmented distribution lead to extinction?

With increased human activities a fragmentation of most wildlife habitats has occurred and led to the increased isolation of many plant and animal subpopulations. This occurs on different scales. The cultivation of natural land has caused most of this isolation, where exploitation of, e.g. peatlands and woodlands, leaves only small remaining fragments of natural land.

The crucial question is if there is any gene flow between geographically more

or less isolated populations. Can gene flow occur even if some kind of geographical barrier, such as vast agricultural districts or densely human populated land areas, separates them? Spores can in theory be carried by wind over vast distances. And what geographical distance *does* imply isolation for species that produce small and easily spread spores?

The disjunct distribution of many species may, in many cases, be explained by relict ranges from a time period of more continuous distribution range and suitable climate, but also by the poorly known 'real' distribution range and/or the poorly understood taxonomy of the species.

An example of a species with climatological relictual sites is the oceanic *Campylopus atrovirens* De Not., which still have exist some small isolated subpopulations outside its main climatic range (westernmost Europe) in Southern Sweden. Also relictual subpopulations of alpine species in the temperate lowlands of South Sweden can persist for a long time, for example the alpine *Rhytidium rugosum* (Hedw.) Kindb. and *Tetralophozia setiformis* (Ehrh.) Schljak.

The disappearance of subpopulations from geographically and climatically marginal or isolated relict localities can reduce the total range. This has happened for some glacial relicts that have vanished from the European lowlands, like the alpine wetland mosses *Meesia longiseta* and *Warnstorfia sarmentosa.* (Wahlenb.) Heden. Also some rocky outcrop species like *Anomobryum julaceum* (Gaertn. & al.) Schimp.*, Conostomum tetragonum* (Hedw.) Lindb., *Oedipodium griffithianum* (Dicks.) Schwaegr. and *Tetralophozia setiformis* have disappeared from some relict sites below the alpine zone in Sweden, probably caused by climatic changes.

However, a population can be very old

The survival of a geographically isolated population can be described using the following properties: (1) the habitat quality of the sites; (2) the population size, and (3) the site context (i.e. how sites are situated in relation to the nearest site, and in which type of matrix). The last two together describe the grain and juxtaposition of sites in the landscape (ANGELSTAM 1992).

Most perennial bryophytes probably have, at least in theory, an almost infinite lifespan and can form immense clones by vegetative spread alone. They may sooner or later produce archegonia, antheridia and, if fertilisation is successful, sporangia are produced. LONGTON & SCHUSTER (1983) gave an example from North America of a population of *Anastrophyllum saxicola* (Schrad.) Schust. that had cloned for some thousands of years. The extent of the clone suggested that a minimum of 2,000 years had elapsed since its initiation. The ability to survive as clones is of importance for allowing numerous bryophyte taxa to persist for long periods and even under suboptimal conditions (LONGTON & SCHUSTER 1983). Populations living under stable conditions and without reproduction can persist as 'living fossils' for many years before eventually becoming extinct.

Long-term survival at a site is therefore extremely difficult to estimate without good demographic information and may vary substantially according to climatic and other environmental conditions – not to forget the effect of man-made impact. Demographic studies have been made on very few taxa, e.g. *Polytrichastrum formosum* (Hedw.) G.L.Sm. (LANGAAS 1997) and *Hylocomium splendens* (Hedw.) Schimp. (ØKLAND & ØKLAND 1996) and more demographic information is needed (BISANG & HEDENÄS 2000).

However, a species can survive a long time in a spore bank

Even if diaspores can survive for some time in the soil, we still know very little about the longevity of the diaspore bank (cf. van TOOREN & DURING 1988). However, it is known that some species in boreal ecosystems are established from a diaspore bank in soil (JONSSON 1993) and the longevity of diaspores in soil can, theoretically, be up to 100 years (SÖDERSTRÖM 1995).

Spores usually survive drought better than other diaspores, such as vegetative propagules and leaf fragments, and the longevity of spores is generally better than gametophytic bodies. The longevity of spores in dry storage shows considerable inter-specific variation and depends greatly on the conditions of storage. Longevity in these conditions may be anything from a few days to many years (LONGTON & SCHUSTER 1983). *Oedipodium griffithianum*, which occurs in the alpine region of Sweden on rather isolated mountain peaks, is reported to have spores of very high longevity, 20 years (CHALAUD 1932).

We have to consider the spore bank as a buffer or reserve that could potentially be the last chance for species very close to extinction. As long as we do not know to what extent a viable spore bank exists, the precautionary principle must be used, and the presence of a viable spore bank should not, therefore, automatically be assumed.

How can small subpopulations increase the risk of extinction?

A species with a small population is more vulnerable to stochastic events than one with a large size. Different reasons may account for small population sizes. The size of habitat is one, but also loss of habitats and degradation of habitat are among the most frequent threats. There may also be a combination of reasons, both natural and man-made. Most species are rare only in part of their range (mostly at the edges of their distribution) while others are rare throughout their range.

Another situation concerns species that require highly specific and space-limited substrates for their development. The occurrence of small, very scattered, patches of substrates, for example, periodically wet hardwood is a characteristic substrate for the dioicous hepatic *Scapania glaucocephala* (Tayl.) Aust. In Sweden, it has been found only on 2-3 logs in a swamp forest in a calcareous district (BRATT 1999). Species confined to that kind of dead wood in a rare environment may locally show rather high population sizes in a given time.

However, the crucial point is that the combination of suitable substrate and environment probably must be present in sufficient amounts on both temporal and spatial scales.

Another case is provided by a forest-gap species. A species only persists in small forest gaps for a few years. Thus, the unpredictability of gaps in space and time implies large fluctuations in population size. Consequently, in the above-mentioned cases it may be better to focus on preserving the appropriate forest stand dynamics within an area large enough to avoid extinction than focusing on the number of individuals (NILSSON & ERICSON 1992).

Does the size of the locality matter?

Moose dung with *Splachnum melanocaulon* (Wahlenb.) Schwaegr., a maple tree with *Cryphaea heteromalla* (Hedw.) Mohr, a calcareous ravine with *Neckera besseri* and a mountain peak with *Oedipodium griffithianum* are localities of different sizes but all with rare taxa. Obviously, a large locality may theoretically support a larger population of a species than a small one. However, in a situation involving protection, it is not certain that a single large reserve is better than several small ones with the same total area. In conservation action it is not always be cost effective to put all efforts into one locality. It may instead me more safe to spread the risk (protection measures) and to protect several different localities.

Ideally, we ought to know more about the area requirements of each species before resources are put into protection of land. The minimum size of a site needed for the species to survive differs obviously between taxa. However, exploitation of land and water seldom waits for the scientists to decide the best solution. Meanwhile, as many known viable sites as possible should be protected for those species that are considered to be threatened (HALLINGBÄCK 1995).

If a locality decreases in size the proportion of the edge zone increases. Increasing the edge zones make the locality more vulnerable to negative extreme climatic influences such as drought, which may damage species such as the liverwort *Harpanthus scutatus*, but also to invasion by weedy species, e.g. *Hypnum cupressiforme* Hedw. and *Brachythecium oedipodium* (Mitt.) Jaeg. For example, OLSEN (1988) documented that edge effects penetrated 100 m or more into boreal forest. Further, species with highly specific demands for a stable microclimate are usually sensitive to edge effects. For example, felling of the surrounding forest resulted in a 50% population decline of *Didymodon glaucus* Ryan at its only known site in Sweden (HALLINGBÄCK 1998).

CONSERVATION PRIORITIES BETWEEN NATIONAL, EUROPEAN AND GLOBALLY THREATENED SPECIES

To sum up the discussion, it is clear that many bryophytes theoretically have a very high potential capacity for survival, especially if spores are produced in abundance, if suitable habitat quality is still available. However, the cause of

regional rarity of spore-dispersed taxa may be a combination of many circumstances both in time and space, e.g. a period of air pollution, or lack of suitable substrate, e.g. *Neckera pennata*.

The three groups of European non-endemic rare species listed in the beginning are 1) rare in the whole world (e.g. *Distichophyllum carinatum*, fig. 1); 2) rare only in Europe (e.g. *Bryhnia novae-angliae*, fig. 2); 3) rare within the main part of its European distribution area, with the exception of one or few smaller parts where the species does not seem to be threatened (e.g. *Buxbaumia viridis*, fig. 3). In reality, it is impossible to give general recommendations to prioritise between these three groups. To start with, one important concern is to know whether the rarity and/or decline is caused by man or is 'natural'. For those species where we know the causes of the threat, the implementation is much easier to suggest, regardless whether the species is threatened or rare only in small part of Europe or in the whole world. In brief, estimation of the long-term survival of these species and the suggested conservation action has to be decided on a species-by-species basis. This is mainly because of the different sensitivity to changes in the environment, reproductive capability, and diaspore dispersal distance used by each species. Further, the habitat quality requirements of different species have seldom been studied among bryophytes and urgently need to be studied in greater detail. Bryophyte species that produce spores, at least now and then, seem to tolerate a higher degree of habitat fragmentation compared with many animals. However, there is a limited chance to survive if the subpopulations are very small and restricted to sites under severe human impact.

There are certainly very many crucial questions still to be answered before we can make general recommendations regarding the need for better conservation for regionally rare and declining species.

Finally, we should not forget that there is always national pride among the citizens of a country to take care of all their country's native species, regardless of whether they are more common in other countries. However, from a global conservation point of view there is an international responsibility aspect that urges each country and region to give highest priority to those species of their flora and fauna that are unique in order to minimise the risk of species extinction.

FOUR ARGUMENTS WHY EUROPEAN, AND NOT ONLY A GLOBAL, RED-LISTING OF BRYOPHYTES IS NEEDED ARE GIVEN BELOW

1. There is sometimes value in conserving populations at the edge of their distribution range and isolated populations (disjunction) – genetic variation and speciation (BISANG & HEDENÄS 2000).

2. "Preventive medicine" avoiding a critical situation – It is easier to maintain a population when it is still healthy, than to save one at the brink of extinction.

3. The political willingness to act NOT ONLY 'globally' but ALSO locally. Especially concerning large glamorous species (e.g. *Hookeria lucens* (Hedw.) Sm.).

4. The 'precautionary principle' in the conservation strategy for species about which we still lack information.

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