Zeitschrift: Cryptogamica Helvetica

Herausgeber: Schweizerische Vereinigung für Bryologie und Lichenologie Bryolich

Band: 18 (1995)

Artikel: Bryophyte conservation : input from population ecology and metapopulation dynamics

Autor: Söderström, Lars

DOI: https://doi.org/10.5169/seals-821128

BRYOPHYTE CONSERVATION – INPUT FROM POPULATION ECOLOGY AND METAPOPULATION DYNAMICS

LARS SÖDERSTRÖM
Department of Botany, University of Trondheim, N-7055 Dragvoll, Norway

SUMMARY — There are several criteria that can be used for classifying a species as rare and/or endangered. These criteria can be based on the geographical distribution, density of localities, and population biology of the individual species. Rarity may be natural or human-induced and the difference between rare and threatened are emphasized. Attributes of different kinds of rare species are explored, especially the population biology and the relation between habitat dynamics and population biology. It is shown that static protection of single localities where the species occurs in abundance, e.g., in nature reserves, is not always enough to secure the long-term survival. This is especially the case for species in dynamic habitats and species relying on continuous creation of new habitat patches.

KEYWORDS — Rarity, population dynamics, population biology

ZUSAMMENFASSUNG — Moosschutz – Beiträge der Populationsökologie und Metapopulationsdynamik

Es gibt mehrere Kriterien, die für die Einstufung einer Art als 'selten' und/oder 'gefährdet' verwendet werden können. Diese Kriterien können auf der geographischen Verbreitung, der Dichte der Vorkommen und der Populationsbiologie der einzelnen Arten beruhen. Seltenheit kann natürlich sein oder durch den Menschen verursacht; der Unterschied zwischen 'selten' und 'gefährdet' wird hervorgehoben. Eigenschaften der verschiedenen Typen seltener Arten werden untersucht, besonders die Populationsbiologie und die Beziehung zwischen Lebensraumdynamik und Populationsbiologie. Es wird gezeigt, dass statischer Schutz einzelner Orte, an denen eine Art reichlich vorkommt, z. B. in Naturschutzgebieten, nicht immer ausreicht, um das langfristige Überleben zu sichern. Dies gilt besonders für Arten in dynamischen Lebensräumen und für Arten, die auf laufendes Entstehen neuer Flecke des geeigneten Lebensraumes angewiesen sind.

What is rarity?

Rarity is a natural phenomenon, as is extinction of species. Species have died out and new species appeared continuously during the history of evolution. Although mass extinctions have occurred during the past, the extinction rate today is higher than ever, because of human activities. It is therefore necessary to separate natural extinction from extinction induced by human activities and to make a clear distinction between species that are rare for natural reasons and those that are rare due to human activities.

The terminology of rarity is confusing. The most used threat categories today are those of IUCN (e.g., Davis & al. 1986), i.e. Extinct, Endangered, Vulnerable, Rare, Indeterminate, Out of danger and Insufficiently known. These categories are all meant to include a portion of human-induced threat. The official IUCN threat categories are now changed to Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable and Lower Risk, i.e. the term rare will no longer be used (IUCN 1994). The IUCN terms are threat terms and do not cover all types of rarity and there is a need for a refined terminology which emphasizes what is natural and what is human-induced rarity. An alternative use of rarity terms emphasizing this is summarized in Tab. 1. With this definitions of the terms, **rare** species should occur in small populations, low abundances and/or over limited areas. Rare species are not necessarily threatened with extinction because of human activities but may be threatened by the stochastic events that occur in small populations. The number of extinctions among rare species should be on the same level under conditions with or without human impact. A **threatened** species should be negatively affected by some human-induced factor so that the range and/or the population sizes are decreasing. A species may also be threatened if the production of new diaspores or the chance to establish from diaspores are decreasing. If different threat categories are

<table>
<tr><th>Term</th><th>IUCN
(from Davis et al. 1986)</th><th>IUCN
(IUCN, 1994)</th><th>Proposed definition
(used in this paper)</th></tr>
<tr><td>Disappeared</td><td></td><td></td><td></td></tr>
<tr><td>Extinct</td><td>Taxa which are no longer known to exist in the wild after repeated searches of their type localities and other known or likely places</td><td>No reasonable doubt that the last individual has died</td><td>Globally extinct taxa</td></tr>
<tr><td>Vanished</td><td></td><td></td><td>Locally or regionally extinct taxa</td></tr>
<tr><td>General terms</td><td></td><td></td><td></td></tr>
<tr><td>Rare</td><td>Taxa with small world populations that are not at present Endangered or Vulnerable, but are at risk.</td><td></td><td>Taxa that occur in small populations, low abundances and/or over limited areas.</td></tr>
<tr><td>Threatened</td><td></td><td></td><td>Taxa that are negatively affected by human activity.</td></tr>
<tr><td>Threat categories</td><td></td><td></td><td></td></tr>
<tr><td>Critically endangered</td><td></td><td>Facing extremely high risk of extinction in the wild in the immediate future</td><td rowspan="2">Taxa that are rare and threatened</td></tr>
<tr><td>Endangered</td><td>Taxa in danger of extinction and whose survival is unlikely if the causal factors continue operating.</td><td>Facing high risk of extinction in the wild in the near future.</td></tr>
<tr><td>Vulnerable</td><td>Taxa believed likely to move into the Endangered category in the near future if the causal factors continue operating.</td><td>Facing high risk of extinction in the wild in the medium-term future</td><td rowspan="2">Taxa that are threatened but not (yet) rare.</td></tr>
<tr><td>Lower Risk</td><td></td><td>Taxa that are evaluated, do not satisfy the criteria for any of the categories above, and are not Data Deficient.</td></tr>
<tr><td>No threat</td><td></td><td></td><td></td></tr>
<tr><td>(Without specific term)</td><td></td><td></td><td>Taxa that are rare but not threatened</td></tr>
<tr><td>Common, not threatened</td><td></td><td></td><td>Taxa that are neither rare nor threatened</td></tr>
</table>

TABLE 1. Comparison between the use of rarity terms in this paper and by IUCN.

distinguished, the following separations must be made. A clear differentiation between species that are globally extinct and those that are extinct only regionally or locally is necessary. The latter may very well re-establish from a distantly dispersed diaspore if the right conditions occur again. A better term for them is thus **vanished**. The term **extinct** should then be reserved for globally extinct species, i.e. those lost for ever. There must also be a clear separation between threatened species that are rare and threatened species that are not (yet) rare. The former may be termed **endangered** (and/or **critically endangered**) and the latter **vulnerable** (and/or **lower risk**) (Tab. 2). It must, however, be added that it is often difficult to distinguish between endangered species and species that are rare due to natural reasons. Rare species may also be endangered due to their sensitivity to a small decline in population size. A single, unexpected human activity may, e.g., wipe out the whole population or force the population size under the minimum viable size. In addition, some man-induced extinction must be regarded as natural, in the same way that other animals drive species to extinction.

	Threatened	Not threathened
Rare	Endangered	*(Without specific term)*
Not rare	Vulnerable	Common

TABLE 2. Proposed relations between terms describing natural rarity and threat by human activity.

There are several ways of classifying a species as rare. This may be illustrated by the work of Rabinowitz (1981) (Tab. 3). She distinguishes three variables by which a species may be rare: limited geographical ranges, narrow habitat requirements or small local populations (or combinations of these). Species with limited geographical ranges have always attracted botanists and there is a lot of literature on endemism and endemic species. Endemic species occur most frequently on islands and other geographically isolated areas, but they may be found on larger land masses as well. One example of the latter is *Marsupella andreaeoides* (nomenclature follows Söderström & al. 1992) which is confined to western Scandinavia (Fig. 1). Species with narrow habitat requirements may be found scattered over a large geographical range. How scattered they are depends to a large degree on the scale that the habitats are distributed on. A number of species are associated with copper and thus occur only in areas with copper-rich bedrock (or sometimes on copper statues), e.g., *Cephaloziella massalongi* (Fig. 2). Species living on dung of large ungulates also have narrow habitat requirements but these habitats are distributed on a finer spatial scale. Different reasons may account for small population sizes. There may be a combination with the second criterion if a species is confined to a substrate occurring in small, very scattered patches that cannot host large populations. Other species colonize successional substrates that may disappear before the species have built up large populations. It is difficult to find examples of bryophyte species in this group, but at least in Scandinavia, *Splachnum rubrum* occurs in this way. The three mentioned criteria may be combined in all combinations, resulting in eight groups, out of which seven can be regarded as rare in one way or another (Tab. 3). The only taxa not rare are those occurring over a large geographical range with wide habitat requirements and large local populations. I have seen no published attempt to classify bryophytes into these groups of rarity but such a classification would be

Geographical range	Large		Small	
Habitat specificity	Wide	Narrow	Wide	Narrow
Local population size				
Large, dominant somewhere	Common	Rare	Rare	Rare
Small, non-dominant	Rare	Rare	Rare	Rare

TABLE 3. The seven forms of rarity recognized by Rabinowitz (1981).

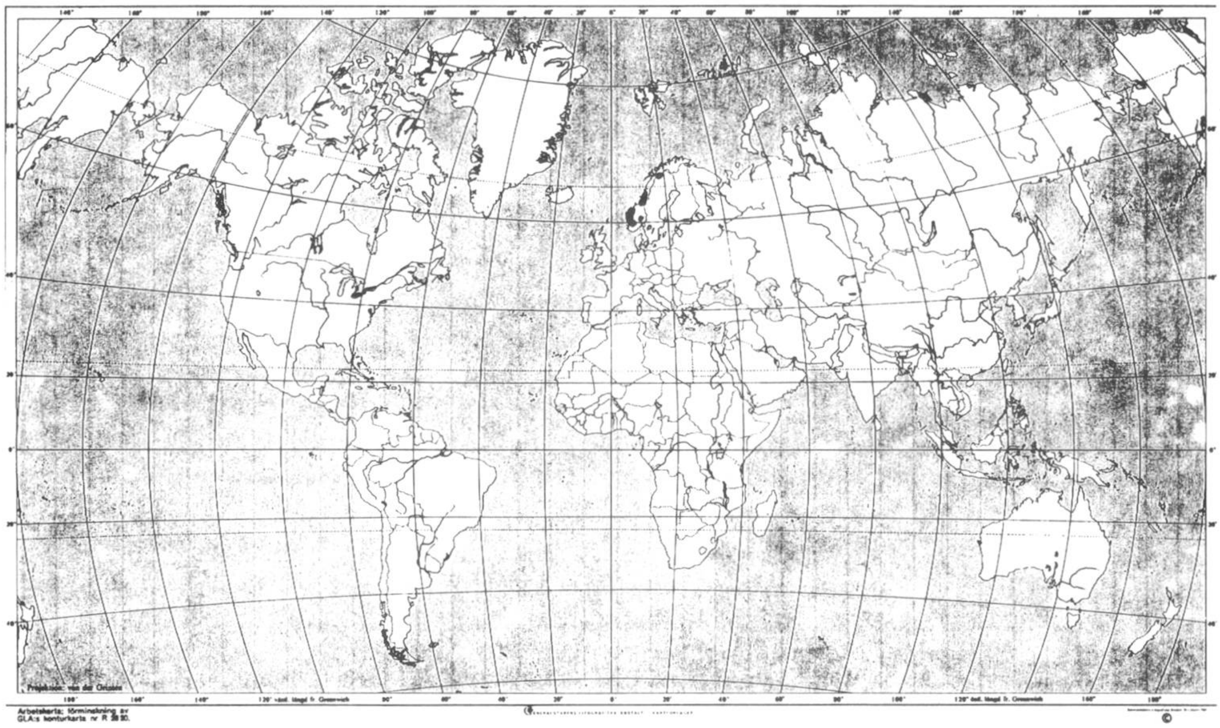

FIGURE 1. World distribution of *Marsupella andreaeoides.*

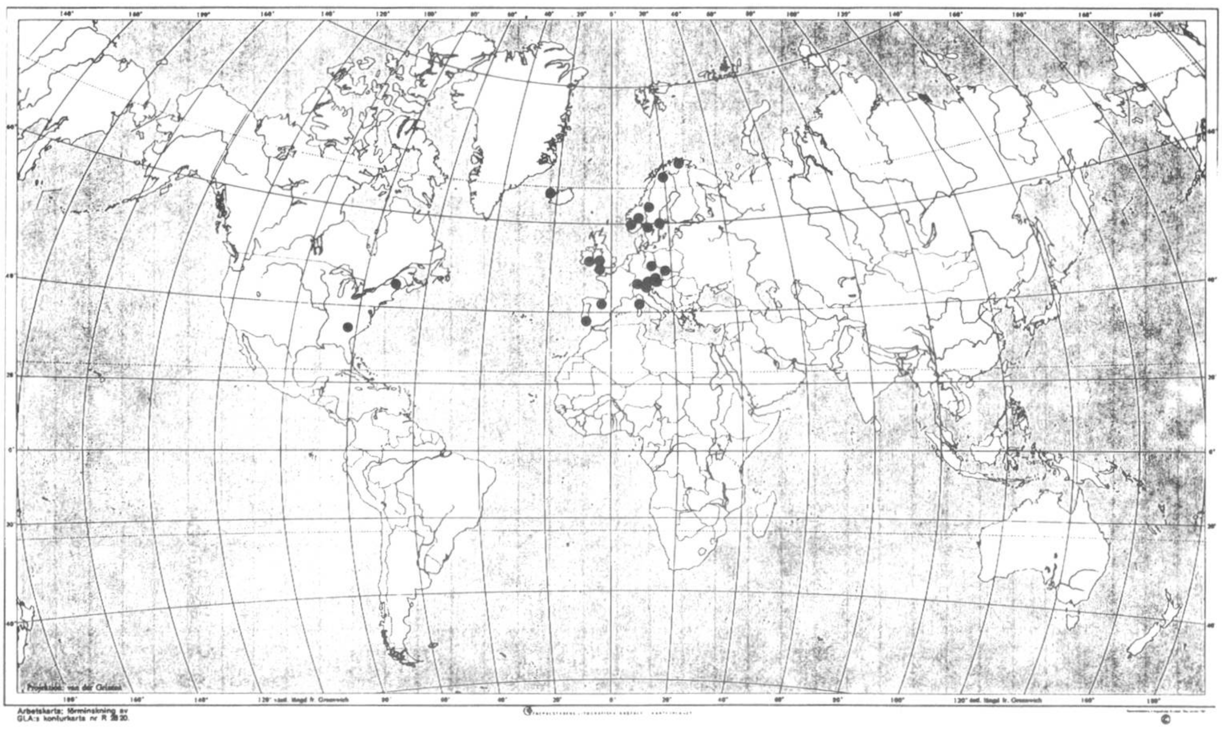

FIGURE 2. Word distribution of *Cephaloziella massalongi.*

interesting, especially if the classified species were analysed further, e.g., their life history strategies, leading to an increase of our understanding of the causes of the different sorts of rarity.

Another aspect of rarity is the frequency and abundance distribution of a given species within its geographical distribution. Most species are rare only at certain localities or in a part of their range (mostly at the margins of their distribution) while others are rare throughout their range. Schoener (1987) calls the former *diffusive rarity* and the latter *suffusive rarity*. Rabinowitz (1981) regards suffusive rarity as *genuine rarity* and diffusive rarity as *pseudo-rarity* and does not incorporate the last group in her seven forms of rarity. For full understanding of the local Red Data Lists the occurrence and frequency (and possible threat) outside the study area of the species included, should be indicated. A preliminary study of the hepatics on the Red Data Lists of Sweden and Norway is approaching this (Weibull & Söderström 1995).

Attributes of rare and endangered species

To understand why species are rare and/or threatened, it is necessary to know the biology of the species concerned in as much detail as possible. This is essential for evaluation of the appropriate conservation steps. Investigations among threatened larger animals have shown that with sufficient knowledge of population ecology, some simple actions may ensure their survival. Such investigations are almost non-existent among plants (although the problem has been recognized, e.g., Cornelius 1991, Söderström & al. 1991), and no such study has been made for bryophytes. Most studies dealing with rare bryophytes so far, concern their habitat requirements and sensitivity to changes in external conditions, e.g., the study of *Neckera pumila* (Hallingbäck 1989). There are only a few studies on the population biology of bryophytes and I am not aware of any study that has been published on the population biology of a rare or endangered bryophyte species. Life history strategies and reproductive biology must be known in much more detail for decline of the species to be understood (cf. Söderström 1994, Longton 1994). Such studies are badly needed for an effective conservation of endangered bryophytes.

Bryophytes live in habitats that are more or less dynamic. In the most extreme cases, the substrate appears and disappears again so rapidly that the species living on them may only go through a single or a few life cycles. This is true for many species on decaying wood (Söderström & Jonsson 1992) and even more for species on dung. Such species must be efficiently dispersed so that they can reach new localities easily. The life history strategies that are favourable for a certain species differ with different substrate dynamics. Two features of dynamic habitats are important; the time that they last and the regularity with which they reappear (both in time and space; During 1979). In short-lasting habitats it is important to produce as many diaspores as possible in a short period of time while species on substrates lasting for longer periods may invest more in growth before they start to reproduce. Some short-lasting substrates are more or less continuously present where they occur, e.g., decaying wood and dung, while others may appear at more irregular intervals, e.g., uprooted trees in forests (Söderström & Jonsson 1992). Most of the bryophytes on forest floors establish on the more or less bare soil under uprooted trees (Jonsson & Esseen 1990) and most species establish from the diaspore bank (Jonsson 1993). All of them need not be present in the extant bryophyte cover at any time. Living trees do not collect and store diaspores of epixylic species. Therefore, when a tree falls down and starts to decay, epixylic species must colonise it by distantly dispersed diaspores. A viable population of epixylic bryophytes must, thus, always be present in the surroundings as gametophores (or sporophytes).

The spatial pattern in which a temporary substrate occurs (and re-occurs) is also important. If suitable conditions reappear on the same spot after some time, a strategy of mainly local diaspore deposition is favoured. Such species do not need to produce easily transported diaspores, but may instead invest in the production of larger spores that are more easily established. *Riccia* species are good examples for this. Such species may be very locally dispersed since their distance dispersal ability is limited. That may be the reason why many *Riccia* species appear on Red Data lists. If instead the chance is greater that suitable conditions appear on another spot, the favoured strategy must be to invest in efficient transport mechanisms and less in establishment ability. In bryophytes, this mostly corresponds to a large number of small, easily wind-dispersed diaspores.

This raises an important question for the conservation of bryophytes. Should species with viable diaspores in the diaspore bank, but without mature gametophores, be considered extinct/vanished? They may, at least theoretically, establish new shoots in 10, 50 or 100 years. And are such species rare if only 2 shoots appear each year but hundreds of thousands of viable diaspores are present in the soil? In an extraordinary year, thousands of new shoots may be present. Some species may survive just because of such extraordinary years, which replenish the store of viable diaspores.

Regional dynamics in bryophyte metapopulations

To secure a species it is necessary to consider not only the local population sizes but also the spatial dynamics, i.e. the process of metapopulation dynamics. This theory says that spatially separated populations are dependent on each other through occasional dispersal. If the local dynamic is high (and populations are small), local extinctions are to be expected (cf. Hanski 1991). These localities can only be recolonized from other populations. Distribution and local abundance are intimately linked in such cases. Large local populations produce a larger number of diaspores than small populations of the same species. If the chance that some diaspores will disperse to and establish at a new locality is large, then most of the suitable localities in a region will be occupied (cf. core species *sensu* Hanski 1982). If a majority of the localities are occupied, the total number of diaspores produced in the region is high and the chance is large that a locality where the species has disappeared will be recolonized. This means that if human activity reduces the number of localities for a species or the local population sizes so that the extinction rate increases and recolonisation rate decreases, the populations will decline and the species will eventually become endangered (see also Lawton 1993 for a general discussion of the topic).

A disturbance of the regional dynamics of a smaller part of the populations may cause a severe decline in the total population size if the populations function as a source-sink-system (*sensu* Pulliam 1988). In such systems source areas function as centres for dispersal where the number of diaspores produced exceeds the number that is needed to replace individuals that die. Those areas can "export" individuals. Sink areas are habitats or areas where the number of produced diaspores is smaller than the number needed for replacement of dead individuals, so the populations will decrease and die out without support of diaspores from source areas. If sink areas do have just a small negative growth rate, this may be a slow process possibly lasting over many years, and a low number of successful diaspores from outside is able to balance the death rate. Such species may survive even if they have the majority of their populations in sink areas. In a theoretical exemple, Pulliam (1988) showed that the source populations may under some circumstances be only a small portion of the total population (10%). However, the consequences are fatal for such species if the source populations are wiped out. In the example above, only 10% of the whole population are enough to extinguish it if these are the 'wrong' 10%.

The occurrence of safe sites or source areas may also be looked upon with a temporal scale, i.e. variation between years. Examples of this may be *Anastrophyllum hellerianum* and *Lophozia ascendens* in a forest in northern Sweden where I saw them for the first time in 1981. The following summer, 1982, was very dry and none of the species was seen. In the following, more normal years they appeared again and the populations increased gradually. The year 1987 had an extremely wet summer and autumn and the production of capsules and spores was extremely high. In the autumn of that year, both species were also found on very open sites where they do usually not occur. In the following years, both species were common but their abundance decreased gradually. This shows that the forest cannot serve as a source area for these species when conditions are unfavourable but may do so during favourable years. The most important source areas for them are the wet or moist forests where they can survive also during bad (i.e. dry) years. If all of these are destroyed, the species will vanish as soon as the next dry year occurs.

Conclusions

Rarity and extinction are natural phenomena. The only reason that we need to be concerned about extinction is that the extinction rate has increased to such a high level due to human-induced activities that evolution can not balance. The overall biodiversity is today rapidly decreasing in a way that is unknown in the history of life. To conserve bryophytes effectively and to assess conservation priorities, it is necessary to distinguish between natural and human-induced rarity, as well as between different kinds of rarity. Therefore, we must increase our knowledge about each species, both about its habitat requirements and its life history strategies.

The goal in conservation must be to conserve ecological and evolutionary processes to a much higher degree than we do today, and in that way also to conserve species and biodiversity. With the limited resources for conservation available today, two aspects of conservation must be emphasized. First, it is important to identify key areas (source areas) for each species and conservation must be directed towards protection of these rather than towards protection of localities with large populations. Secondly, steps must be taken to secure species in areas with human activities since possibilities for creating nature reserves are limited.

Acknowledgements

I would like to thank the organizers of the Symposium on 'Conservation of Bryophytes in Europe - Means and Measures' for the invitation to present this paper, Irene Bisang and two anonymous reviewers for valuable comments on the manuscript, and Carolyn Baggerud for checking the English.

References

Cornelius R. 1991. Zur Bedeutung populationsbiologischer Forschung für den speziellen Naturschutz. *In*: B. Schmid & J. Stöcklin (eds). *Populationsbiologie der Pflanzen*. Birkhäuser, Basel, 298-310.

Davis S. D., S. J. M. Droop, P. Gregerson, L. Henson, C. J. Leon, J. L. Villa-Lobos, H. Synge & J. Zantovska 1986. *Plants in danger. What do we know?* IUCN, Gland & Cambridge.

During H. J. 1979. Life strategies of Bryophytes: a preliminary review. *Lindbergia* 5: 2-18.

Hallingbäck T. 1989. Bokfjädermossa, *Neckera pumila*, en försurningshotad mossa [*Neckera pumila*, a moss threatened by acidification in south Sweden]. *Svensk Bot. Tidskr.* 83: 161-173.

Hanski I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210-221.

Hanski I. 1991. Single species metapopulation dynamics: concepts, models and observations. *Biol. J. Linn. Soc.* 42: 17-38.

IUCN Species Survival Commission 1994. *IUCN Red List Categories*. (s. loc.).

Jonsson B. G. 1993. The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. *J. Veg. Sci.* 4: 819-826.

Jonsson B. G. & P.-A. Esseen 1991. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *J. Ecol.* 78: 924-936.

Lawton J. H. 1993. Range, population abundance and conservation. *Trends in Ecology and Evolution* 8: 409-413.

Longton R. E. 1994. Reproductive biology in bryophytes. The challenge and the opportunities. *J. Hattori Bot. Lab.* 76: 139-172.

Pulliam H. R. 1988. Sources, sinks, and population regulation. *Amer. Nat.* 132: 652-661.

Rabinowitz D. 1981. Seven forms of rarity. *In:* H. Synge (ed.). *The Biological Aspect of Rare Plant Conservation.* Wiley, Chichester, 205-217.

Schoener T. W. 1987. The geographical distribution of rarity. *Oecologia* 74: 161-173.

Söderström L. 1994. Scope and significance of studies on reproductive biology of bryophytes. *J. Hattori Bot. Lab.* 76: 97-103.

Söderström L. & B. G. Jonsson 1992. Naturskogarnas fragmentering och mossor på temporära substrat [Fragmentation of old-growth forests and bryophytes on temporary substrates]. *Svensk Bot. Tidskr.* 86: 185-198.

Söderström L., T. Hallingbäck, L. Gustafsson, N. Cronberg & L. Hedenäs 1991. Bryophyte conservation for the future. *Biol. Conservation* 59: 265-270.

Söderström L., L. Hedenäs & T. Hallingbäck. 1992. Checklista över Sveriges mossor. *Myrinia* 1: 13-56

Weibull H. & L. Söderström 1995. Red Data Listed hepatics of Scandinavia in a regional and world-wide perspective – A preliminary study. *Cryptog. Helv.* 18: 57-66.