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Bryophyte rarity viewed from the perspectives of life history strategy and metapopulation dynamics

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SUMMARY

Most studies on population ecology of bryophytes have involved common species. However, some studies have compared life history strategies in rare and common species. We review the life history strategies (life expectancy, sexual and asexual reproduction, spore production, spore size and dispersal) for species that are rare in relation to pattern and persistency of suitable habitat patches. In particular, we discuss the dynamics on two levels, within and among localities, for different categories of rare species. We predict that most rare species will be found to have restricted dispersal capacities but higher than average life expectancies of local subpopulations. Natural rarity is distinguished from human-induced rarity and species rare for the latter reason are distinguished as 'threatened'.

KEYWORDS: Bryophytes, rarity, population dynamics, life history strategies.

INTRODUCTION

There are many types of species rarity and species may be rare at different scales. Some species are rare all over their distribution range while others are rare only in part of it, usually at their distribution limits (*diffusive rarity* of Schoener, 1987; *extraneous species* of Hedderson, 1992). Barkman (1968) and Rabinowitz (1981; also see Rabinowitz, Cairns & Dillon, 1986) pointed out that when rarity is thought about in general terms it is not possible to get a clear picture of the phenomenon. Classifications of types of rarity are primarily based on distribution patterns of the species (both spatial and ecological), and thus are fairly static. Birks *et al.* (1998) analysed the British bryophyte flora in terms of Rabinowitz's categories (Rabinowitz, 1981), and found that most rare species are characterized by narrow habitat specificities and small population sizes. Their review of palaeobotanical studies shows that bryophyte species of all major habitat types can migrate and colonize newly created habitats with remarkable speed. This would suggest that rarity of species is determined mainly by rarity of the specific habitats, i.e. they are habitat-limited (cf. Herben, Rydin & Söderström 1991). This contrasts with the results of Longton (1992) and Laaka-Lindberg, Hedderson & Longton (2000), who found that, at least for dioecious bryophyte species, rarity is strongly linked to low or absent sporophyte production, suggesting dispersal limitation, at least for some species.

It is important to ask why a species is rare, but there are other equally important questions. For example, through what mechanism is a particular species rare? How did it become rare? By what mechanisms does a rare species continue to maintain itself? As soon as one starts to ask questions of this kind it becomes obvious that population-dynamics features like the life spans of local populations, dispersal of diaspores, and their germination and establishment must be considered (During, 2000). In other words, information on distribution needs to be compared with life history strategies and metapopulation concepts.

This review therefore takes the perspective of dynamics in populations and habitats. Life strategies focus on the correlations between life history characters and the dynamics of population and habitat, whilst treating the axis of connectivity between habitat patches rather superficially (long-distance versus 'within the ecosystem'; During, 1979). Metapopulation studies focus on sizes, spatial distribution and dynamics of patches, but they reduce within-patch population dynamics to immigration and extinction rates. We suggest that a combination of both approaches may lead to a better understanding of the

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causes of rarity of particular species and thus, the assessment of the degree to which such a species is threatened.

Most often rarity is looked upon in relation to absolute numbers of, or sizes of, plants or their populations. Another way of looking at rarity is in relation to available localities (Hanski, 1982; Söderström, 1989). *Urban species* only occupy a few of the suitable localities but are always abundant where they occur. *Rural species* can be found at almost all suitable localities, but always in small quantities. *Satellite species* also occur in small populations in addition to occurring only at a few of the available localities. These are all rare in some sense, whereas *core species* (occurring abundantly at all available localities) are the only category of common species in the CURS classification of Söderström (1989). None of these types of rarity is mutually exclusive and a species may be rare on the basis of several criteria. However, the reasons for rarity vary among the different types and thus we cannot generalize too much about the life history strategies of rare species unless we define the type of rarity under consideration.

In this paper, we attempt to add a dimension of population dynamics to the rarity concept. We will first analyse some life-history characteristics that may influence species abundance and distribution and then assimilate these with existing knowledge about habitat parameters and dynamics since these are as important as the population parameters themselves (cf. Söderström & Herben, 1997). Finally, we will discuss whether the approach provides new insights into the rarity question and consider which types of rarity are a consequence of the pervasive influence of modern man.

LIFE HISTORY CHARACTERISTICS AND RARITY

Söderström & Herben (1997) reviewed the life history and habitat parameters important for survival of bryophytes in dynamic, patchy environments. Their analysis shows that long-term persistence of species depends on whether successful immigration (dispersal, germination and establishment) can balance the losses of subpopulations by demographic stochasticity, losses of habitat patches, etc. Obviously, for rare species this balance would appear to be particularly precarious. So, the question arises: do rare species differ from more common species in traits that limit successful dispersal and local maintenance? This question is vital to understanding rarity and threats to the persistence of species.

Longton (1992) and Laaka-Lindberg *et al.* (2000) investigated the role of reproduction for rarity (i.e. numbers of localities) in the British flora, using two levels of rarity, rare in Britain and rare everywhere. We have tried to expand their analysis by looking at some other parameters which may be connected to immigration rates and local persistence of populations, using the British bryoflora (Smith, 1978, 1990; Hill, Preston & Smith, 1991, 1992, 1994). The parameters we have analysed are spore size (≤25 μm, 25–50 μm and 50 μm; often the two latter categories had to be combined, in which case large means >25 μm), frequency of specialized asexual propagules (none, rare or frequent; subjectively assigned) and shoot longevity (short- or long-lived; subjectively assigned). We have analysed hepatics and mosses, and dioecious and monoecious species separately. We have also distinguished between rarity in Britain and rarity world-wide, using more or less the same approach as Longton (1992) and Laaka-Lindberg *et al.* (2000) (Table 1). The parameters analysed are not independent of each other but usually assembled in strategies or syndromes (During 1979, Hedderson & Longton 1995). We have therefore investigated their interdependence on each other (Table 2).

Associations between traits and rarity classes, as well as between the various traits themselves, were tested by contingency analysis of two-way frequency tables, using the G statistic (Sokal & Rohlf, 1995). When expected values for some cells were too small (<5), categories were combined to produce a table that was more suitable for analysis. If lumping was necessary, the following categories were taken together: spores medium-sized + large; asexual reproduction rare + abundant; rare + frequent in the UK; or world-wide rare + disjunct.

Sexual and asexual reproduction

Sexual reproduction. Sexual reproduction is one of the most important features for species survival since it produces both diaspores for dispersal in time and space, and genetic variation. Analysis of correlations in the British flora by Longton (1992) and Laaka-Lindberg *et al.* (2000) showed that non-fruiting species were much more often rare than fruiting species. This applies to dioecious species in particular. Abundance of sporophytes is linked with breeding system so that monoecious species produce sporophytes more often than dioecious species. Interestingly, among the sporophyte-producing species,

Table 1. *Correlation between rarity and life history parameters. The signs (– and +) mean negative and positive correlations, respectively (i.e. species with higher sporophyte frequency tend to be less rare than expected, etc.). The number of signs indicates significance (––– and + + +, $P<0.001$; –– and + +, $P>0.01$; – and +, $P<0.05$; ns, not significant).*

		Hepatics			Mosses			All		
		Mon	Dio	All	Mon	Dio	All	Mon	Dio	All
Sporophyte frequency	World	+	+ +	+ +	ns	+ +	+ +	ns	+ +	+ +
	UK	–	+ +	+ +	ns	+ +	+ +	–	+ +	+ +
Spore size	World	ns	ns	ns	ns	ns	+	ns	ns	ns
	UK	ns	ns	ns	ns	ns	ns	ns	ns	ns
Asexual reproduction	World	ns	+	+	ns	ns	ns	ns	ns	ns
	UK	ns	ns	ns	+	ns	+	–	ns	+
Species longevity	World	ns	ns	ns	–	ns	+	ns	ns	ns
	UK	ns	ns	ns	ns	ns	–	–	ns	+ +

more monoecious than dioecious species were found to be rare. The authors of both papers suggested that not only production, but also genetic variation (presumably less in monoecious selfing species) is important when a species attempts to occupy new habitat patches.

Among the hepatics, large-spored species tend to produce sporophytes more often than expected and small-spored species less often (Table 2). Among mosses, this trend was much weaker and only significant for dioecious and monoecious species together. Species with large spores (both hepatics and mosses) are in addition mainly monoecious.

Asexual reproduction. Asexual reproduction also produces diaspores that may be as important as sexually produced spores for survival of local populations of bryophytes, but since these are genetically identical to the mother plant (except if somatic mutations have occurred; Mishler, 1988) they do not contribute to genetic diversification. They are also mostly larger than spores and therefore assumed to be more difficult to disperse by wind then most spores.

Among hepatics there is no correlation between frequency of asexual reproduction and rarity (Laaka-Lindberg *et al.*, 2000), but in our analysis dioecious species (and all species) without asexual reproduction tend to be more rare world-wide than expected (Table 1). Monoecious (and all) mosses without asexual reproduction tend to be rare in Britain much more often than expected, but only species with short-lived shoots show this trend ($P<0.001$). In contrast to the situation among hepatics, no correlation between frequency of asexual reproduction and world-wide rarity exists for mosses.

Asexual reproduction is, however, often related to other parameters. Thus, dioecious mosses produce asexual propagules much more frequently than monoecious species, but no such trend was found among the hepatics. Frequent asexual reproduction is found more often than expected among species for which sporophytes are unknown in Britain or unknown anywhere, and less often for fruiting species (Table 2). This holds especially for dioecious species. Among the hepatics, no such trend was found. Also spore size seems to be related to asexual reproduction. Small-spored species tend to have asexual reproduction much more often than expected, in contrast to large-spored species (Table 2). Interestingly, this trend was not found for monoecious mosses. For longevity of shoots a similar relationship was found. Hepatics with short-lived shoots possess sexual reproduction more often than expected while hepatics with long-lived shoots show the opposite. Mosses show the same trend. Here monoecious hepatics are the exception.

Dispersal and establishment

Diaspore size influences dispersal ability and establishment. The smaller the spores, the more easily are they transported over longer distances by wind, but larger spores will establish more easily once they have arrived at a locality. Moreover, larger spores tend to survive longer in the diaspore bank (Jonsson, 1993; During, 1997), which may be an important aspect of local population persistence. However, a species with small spores produces, in general, more spores than a species with large spores. This will give

Table 2. *Correlation between life history parameters used to evaluate rarity. The signs (– and +) mean negative and positive correlation, respectively. The number of signs indicates significance level (—— and +++, P<0.001; — and ++, P<0.01; – and +, P<0.05; ns, not significant). Positive correlation for breeding system indicates correlation with dioecism, negative correlation with monoecism.*

			Sporophyte frequency	Spore size	Asexual reproduction	Shoot longevity
Spore size	Hepatics	Dio	++			
		Mono	ns			
		All	+++			
	Mosses	Dio	ns			
		Mono	ns			
		All	+			
Asexual reproduction	Hepatics	Dio	ns	++		
		Mono	ns	++		
		All	ns	++		
	Mosses	Dio	–	++		
		Mono	ns	ns		
		All	++	++		
Shoot longevity	Hepatics	Dio	ns	ns	–	
		Mono	ns	ns	ns	
		All	++	ns	–	
	Mosses	Dio	+	+++	++	
		Mono	–	++	+	
		All	++	ns	++	
Breeding system	Hepatics		++	–	ns	+++
	Mosses		++	+	+++	+++

more chances for success and thus may balance the spore size effect (cf. Eriksson & Jakobsson, 1998). Perhaps due to this balance, spore size showed hardly any correlation with rarity (Table 1). Also spore size appears to be partly correlated with other parameters, as discussed above.

Life expectancy

Life expectancy can be regarded at three levels: individuals (shoots), genets and populations. The life span of a shoot is here regarded as the time over which growth occurs, although each segment of a shoot is only viable for a few years at most. When the whole shoot ceases to grow and growth must restart from asexual diaspores (or spores), it is assumed to be dead. The life spans of shoots may have an effect on population longevity, and may thus be related to rarity. The data, however, do not suggest this strongly. When all bryophytes are considered together, there is a tendency (especially for monoecious species) for species with short-lived shoots to be rare (in the UK) more often than expected, and for mosses which are rare world-wide the same trend was found (Table 1).

Life expectancy of shoots is also related to other parameters, as discussed above. In addition, species with short life spans are more often monoecious and more often produce sporophytes frequently, although the group of mosses for which sporophytes are unknown is also mainly composed of species with short-lived shoots. Most of these produce asexual propagules abundantly, however, which may play an important role in the persistence of local populations. A similar argument may hold for the remarkable result that, in dioecious mosses, small spore size is correlated with short shoot life span, while in monoecious mosses (which propagate vegetatively much less often) species with short-lived shoots and big spores tend to be over-represented. This reflects an uneven distribution of life strategies in which dioecious species tend to be colonists or perennials (*sensu* During, 1979) while monoecious species are mainly annual or short-lived shuttle species (Longton, 1988).

The life span of a population depends on two things, the death rate of individual shoots (gametophores, i.e. shoot longevity) and the recruitment rate. When the recruitment rate is equal to or higher than death rate, extinction of a population can only occur if external forces like destruction of habitats or mechanical destruction kills the whole population. This will cause instant disappearance. When habitats are short lasting (e.g. decaying wood), the disappearance of a substratum patch is pre-determined and with it the population will disappear. In order to survive at a regional scale, new habitat patches need to be colonized at the same rate as old ones disappear. When death rate is higher than recruitment rate, local extinction can occur for purely demographic reasons. This will then be through a gradual decline of the size of population, e.g. in successional communities where recruitment rates decline with time due to changes (biotic or abiotic) to the habitat.

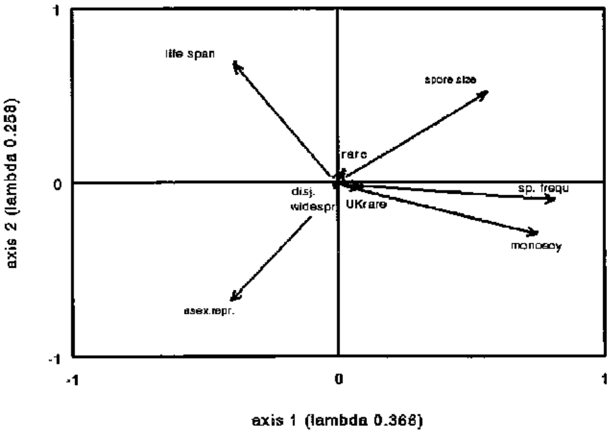

Figure 1. PCA ordination of British hepatics.

Do population longevity, death rate or recruitment rate differ between common and rare species? In most short-lasting habitats both common and rare species can be found, e.g. *Splachnum luteum* and *S. melanocaulon* on dung in northern Scandinavia. However, the more short-lasting is the substratum, then the more efficient must be the re-colonization if the total number of populations is not to suffer a decline in the region (cf. Söderström & Herben, 1997). It is not the diaspore production per individual that is important but the total diaspore production in the area. A rare species must therefore have a higher diaspore production than a common species in order to persist.

Interdependence of parameters

As stressed repeatedly above, the traits studied are not independently distributed over the species. Moreover, some characters (notably spore size) play a dual role with regard to immigration and local persistence. In order to take such interdependencies into account, the two data sets (using only species for which information about spore size was available; excluding rarity categories) were subjected to principal components analysis (PCA, with centring and standardization of variables), followed by correlation of the first two axes with the rarity categories, using the program CANOCO (Ter Braak, 1998). The resulting ordinations are very similar for hepatics and mosses (Figs 1, 2). Breeding system and sporophyte frequency are strongly correlated with axis 1, whereas the second axis is mainly determined by shoot life span and frequency of asexual propagation. The correlations of the rarity categories with the axes are rather low, especially for the hepatics, and the directions of the trends differ slightly between mosses and hepatics. In the ordination of the mosses, rarity world-wide and disjunct distribution correlate with the first axis (with rarity positively correlated with

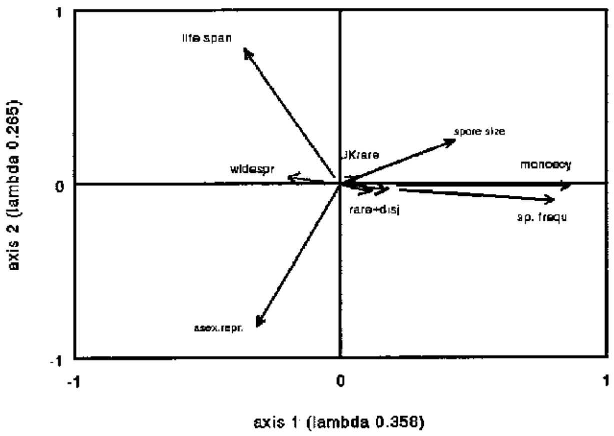

Figure 2. PCA ordination of British mosses.

monoecism and abundance of sporophytes), which suggests Longton's result, that monoecious species frequently produce sporophytes yet are often rare, dominates this correlation (Longton, 1992).

The ordinations also visualize a pattern that may already be evident from the correlations between the individual parameters. Local persistence may be related to long-lived shoots, high frequency of asexual propagules or large spores. These traits tend to be negatively co-varying, which suggests underlying trade-offs between them.

The question as to whether rare species are characterized by specific combinations of traits can be approached from two different perspectives. On the one hand, rarity may be caused by poor immigration capacity in relation to abundance and duration of habitat patches (i.e. may be due to dispersal limitation). In this case one would expect rare species to show a combination of poor dispersal capacity (sporophyte production rare) and short duration of subpopulations/habitat patches. Note again that spore size plays a double role here: large spores tend to be dispersed poorly, but more easily lead to successful establishment.

Alternatively, one could envisage that rare species survive only if they have good immigration capacities to counteract population or habitat loss. Thus, Longton's result that most rare monoecious mosses produce sporophytes frequently (Longton, 1992) may be interpreted in such a way, that only species with this trait are able to survive despite their rarity (which may be due to narrow habitat specificity and rarity of the habitat itself, i.e. they would be habitat-limited). The fact that rare dioecious species show the opposite – very often without or with rare sexual reproduction – may be related to their better capacity to maintain local populations – more frequently with long-lived shoots, more often with asexual propagation, and perhaps better represented in the diaspore bank, which often largely consists of asexual propagules (During, 1997). These species would then be dispersal-limited.

Most comparisons between rare and common species have, like this one, been done by generalizing traits in both categories and comparing them. Such comparisons, however, suffer from phylogenetic constraints upon species. A better method is to compare pairs of related species where one is rare and the other common. This has been tried for vascular plants in agricultural landscapes in Sweden (Eriksson & Jakobsson, 1998; Jakobsson, Ahlgren & Eriksson, 1999) using 18 characters related to distribution, environment, dispersal and life-history strategies. They found that rarity was associated with low abundance in the habitat, a small geographic range, infrequently occurring habitat, being close to the margins of geographical distribution, dependence on disturbance for recruitment, dependence on hay-making or grazing, habitat specialization, a short life span and lack of vegetative propagation. The first two are connected with the type of rarity itself and the next two with habitat distribution. The following three reasons are dependent on habitat quality while the last two are related to population biology. To our knowledge no similar comparison has been made for bryophytes. A preliminary analysis using such phylogenetic independent contrasts of our data sets shows that the correlation between rarity and frequency of sporophyte production is upheld in all cases. Moreover, mosses that are rare worldwide tend to be dioecious, but rare mosses with frequent sporophyte production are nearly all monoecious. Other trends were not supported in the analysis, which is known to be able to detect only very robust trends.

Some case studies

A study of 18 epixylic bryophyte species in northern Sweden (Söderström, 1989) showed that all common (core) species reproduce abundantly with small spores, enabling long-distance dispersal and a high colonization rate of new localities. They also produced large gemmae abundantly, providing high local establishment and thus minimizing the local extinction rate. The only exceptions were *Anastrophyllum hellerianum* (with small gemmae that may be efficient also in distance dispersal) and *Ptilidium pulcherrimum* (without gemmae and with large spores). The latter species, however, produces large numbers of spores and has a low extinction rate (Jonsson & Söderström, 1988). Three of the species, *Barbilophozia attenuata, Calypogeia suecica* and *C. integristipula*, do not produce spores but frequently produced gemmae. They were found in only a few localities but always abundantly (*urban* species) presumably due to restricted distance dispersal but good local persistence. One species, *Cephalozia affinis*, was found at many localities but always in small populations (*rural* species). It produces both spores and gemmae, but in rather small quantities.

Three *Herbertus* species occur in western Norway, and they are all rare (i.e. occurring at few localities, but often with large populations). None produces spores in the region and they reproduce asexually only by fragmentation. Løe & Söderström (2001) found that germination ability of fragments was lower in *H. stramineus* than in *H. aduncus* and *H. borealis*, and that the population sizes at the localities where they occur were also generally larger in the two latter even though *H. stramineus* is the least rare of the three. This may indicate that local populations are expanding through fragmentation and subsequent growth, and in species with lower establishment rate local population growth rate is smaller.

PATTERN AND PERSISTENCE OF SUITABLE PATCHES

Population parameters are important for species survival and thus also for their distribution and abundance (rarity). However, for dynamic populations, population parameters must always be seen in relation to habitat parameters such as habitat quality, persistence, patch size and distribution patterns, and habitat analysis must always form an important part of an analysis of the ability of a species to survive (Söderström & Herben, 1997).

Habitat quality

Traditionally floras have given information on habitat in general terms like 'growing on decaying wood, rarely on peat' or 'on sandy, sometimes clayey soil'. This is information on where the above-ground gametophyte stage can be found, i.e. the habitat where a species can survive, at least for some time and at least sometimes. However, the quality of habitat varies and a species may not fulfil the whole life cycle on all habitats. It is common that species reproduce on some (optimal) substrata although they may grow on others (Söderström, 1994). Examples are *Lophocolea heterophylla*, *Ptilidium pulcherrimum* and *Tetraphis pellucida* which are frequently found on decaying wood, boulders and tree bases, but reproduce sexually much more frequently on decaying wood than on other substrata (Söderström, 1995). In addition, germination and establishment from spores may be successful only under a much more restricted set of conditions than that allowing gametophyte survival (for example, see Miles & Longton, 1992; Sundberg & Rydin, 2002).

Habitat quality may also vary in time. Many bryophyte species need more moisture to germinate than the mature gametophores need to grow. Due to variation in precipitation, some habitats may be available for germination only in some years. An example of this is that of hepatics on decaying wood in moist forests. In a wet forest in northern Sweden, *Anastrophyllum hellerianum* and *Lophozia ciliata* disappeared completely during an exceptionally dry year (1982) and the following years they were much rarer than before although the populations gradually increased. During an exceptionally wet year (1987) they established again everywhere, also on open dry spots where they would never survive a normal year. Over the following normal years they gradually declined (L. Söderström, pers. obs.). In this case not only establishment but also survival of mature plants was dependent on weather conditions. Species sensitive to such events require safe sites where they can survive during poor conditions (source areas, refugia). When discussing habitat specificity, one should therefore try to evaluate how dependent the species is on certain habitats for completing its whole life cycle and for survival of harsh periods. This means that many species will turn out to be much more habitat specific than is usually believed from their often temporay occurrences on suboptimal substrata.

Habitat persistence

Most if not all habitats are dynamic, and suitable patches will persist only for a limited period, although this may be very long for some (cf. Söderström & Herben, 1997). The duration of habitat sets the maximum time available for growth and reproduction. For a population/colony to contribute to the long-term survival of the species, it must produce at least one new colony on another substratum patch during this time. The shorter the substratum life span, the more often must the species disperse to new patches, and the better must be its dispersal efficiency. A species with restricted dispersal ability or a slow growth rate will be dispersal-limited and thus rarely found on a short-lasting habitat (i.e. occupying few of the available habitats; cf. Herben & Söderström, 1992).

Habitat patch size

Habitat patch sizes determine the maximum population size at each locality (Herben & Söderström, 1992). This influences both the local survival probability and dispersal possibilities. Smaller populations are more vulnerable to stochastic extinctions and very small habitat patches are therefore at great risk of disappearing before they have contributed to the long-term survival. Smaller populations also produce fewer diaspores and contribute less to overall dispersal than larger populations, although they may be important as stepping stones between distant larger patches. However, in dynamic habitats this is likely to result in a low number of occupied localities.

Pattern of habitat patches

The geographical distribution of habitat patches is also an important factor. If the distances between suitable patches are large, better dispersal ability is needed. Many habitat patches are random or aggregated with distances between some patches smaller than the average distances. Dispersal within these aggregates may then be possible, even for species with restricted dispersal ability which are unable to disperse between more distant patches. Such aggregates will thus increase the probability for a species to survive (Herben *et al.*, 1991) and species with lower dispersal ability will tend to occur on many of the substratum patches within habitat aggregates where they occur (within some habitat aggregates), but be absent on many of their aggregates.

At the range limits, suitable habitat patches will often be fewer and more scattered. This means for dynamic species that they must disperse more easily between habitat patches to re-colonize them, and this may explain why many species are rare (defined by numbers of localities and population sizes) at their range limits (cf. *extraneous elements* of Hedderson, 1992).

ARE ALL RARE SPECIES THREATENED

For a species to be called threatened, it must be at risk of extinction within a short period of time (cf. IUCN, 2001) if nothing is changed to secure its long-term survival. Not all rare species are threatened with extinction in the near future (Söderström, 1995). Rarity (irrespective of criterion used) is common in bryophytes (e.g. Vitt & Belland, 1997) and populations of many rare species exist for long periods without showing a decline in size. Among species with stable populations, only the rarest (those with the smallest and fewest populations) are at risk due to stochastic events. These events are often external, destroying the whole locality.

However, many initially quite common species have shown a rapid decline in population size to the point of extinction. Even common species like *Hylocomium splendens* decreased by over 50% from the 1950s to 1985–86 in Finland (Mäkipää & Heikkinen, 2003) and the same has been observed in The Netherlands (van Tooren, During & Nieuwkoop, 1995) and should theoretically be included on the Red List. However, the species still occurs over large areas and in such large quantities that a 'red book' listing is not needed. Declining species may decline for two main reasons. First, their habitat may be declining thus reducing the possibilities for establishing large and numerous populations. Secondly, they may decline due to a failure in some stage of the life cycle, e.g. reproduction or dispersal. These two factors are, as shown above, not completely independent. If fragmentation of habitat increases, the dispersal between habitat patches must become more efficient otherwise the distances faced are so large that successful colonization of new patches becomes rarer than the process of local extinction. Populations may also decline for population reasons, but the decline is usually triggered by a change of the environment.

Humans influence bryophyte populations in many ways. The most obvious is the destruction of habitats, effectively reducing the number or size of suitable habitat patches for many species (and increasing it for others). A less obvious influence is the impact on population dynamics, which may lead to reductions in population sizes. Fragmentation of habitats has a profound influence on many bryophytes since it causes both smaller local populations (i.e. increased extinction risk and decreased diaspore population) and increased distance between habitat patches (increased distance to disperse). Thus, a dispersal-limited species may change from being a core species to become an urban species, or even worse, a satellite species (cf. Hansson, Söderström & Solbreck, 1992).

Human influence may also more or less directly affect population biology, e.g. through air pollution. Reproduction of bryophytes is reduced or even stopped in heavily polluted areas (e.g. Raeymaekers & Glime, 1986). In the Netherlands, fertility of *Eurhynchium hians, E. praelongum* and *E. striatum* has declined drastically in the course of this century (Knol & Touw, 1976). Sagmo Solli *et al.* (2000) found that the dwarf males of *Dicranum majus* were absent in some populations in southern Norway where acidification through airborne pollutants was high, while males and sporophytes were common in areas with less pollution. They proposed that dwarf males were more vulnerable to airborne pollution than female shoots. If one episode of extremely acid rain wiped out all males but not the normal-sized females, then reproduction would cease abruptly until new males could be formed by diaspores from outside the area. When reproduction ceases, populations will usually gradually decline since there is no new establishment that can balance natural mortality of shoots or colonies.

CONCLUSIONS

It is usually assumed that a species is rare owing to habitat limitations. However, for bryophytes it seems that population characteristics connected to limited dispersal are often the cause of occurrence at few localities. Such species are in fact dispersal-limited as indicated by the existence of 'empty' localities (cf. Söderström & Herben, 1997). Demonstration of the occurrence of empty localities is technically difficult and requires the use of transplantation/sowing experiments.

Although currently habitat limitation seems to be a much more common cause of rarity than dispersal limitation, human activity may have changed this for many species or will do so in the near future with fragmentation of habitat that increases the dispersal barriers. The problem is, of course, that processes like extinction are subject to a considerable time-lag.

Natural rarity is distinguished from human-induced rarity and species that are rare for the latter reason are regarded as threatened. We hypothesize that most naturally rare species are habitat limited with an ability to survive in small but stable populations. Some naturally rare species may be dispersal limited, but only if the dispersal ability is enough to balance the local extinction rate (cf. Söderström & Herben, 1997). Very often, such species are characterized by a long-lived bank of large spores or asexual propagules in the soil (cf. During, 2000). However, for most decreasing species (which thus are threatened), dispersal limitation may be the reason. When a habitat is fragmented, first the population size decreases due to smaller habitat patches, and the total diaspore production decreases so the number of diaspores available to (re-)colonize a new habitat decreases. In addition, habitat fragmentation often increases the distances between localities which means that better dispersal ability is required to survive.

Taxonomic Additions And Changes: Nil.

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