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RED LISTING OF SPECIES WITH DIFFERENT LIFE HISTORY STRATEGIES

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The aim of Red Lists is to estimate the risk of a species becoming extinct within a certain time. Traditionally, population sizes (local population sizes and/or number of local populations) have been used. However, for many organisms (including bryophytes), occurrences in small but stable populations are frequent and natural. Then the most important aspect is the life history strategies of the species. Important life history parameters to consider are production of diaspores (sexual and asexual), presence of a diaspore bank, dispersal and establishment ability and growth rate. These population parameters must, however, always be treated in relation to habitat parameters such as size, duration, favourability and distribution of patches.
In this paper, population parameters of importance for survival are discussed in relation to habitat patterns and dynamics. A way of evaluating species based on population parameters is proposed.

Key words: Bryophytes, Red list, life strategies, habitat.

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O objectivo das Listas Vermelhas visa estimar o risco de extinção das espécies num determinado período. Tradicionalmente, é tida em conta a dimensão das populações (tamanho por local/número por local). No entanto, para muitos organismos, entre eles os briófitos, é natural e frequente a ocorrência em populações pequenas e estáveis. Assim, um dos aspectos mais importante a ter em conta é a estratégia de vida da espécie. É também importante considerar os diferentes parâmetros biológicos (reprodução sexuada e assexuada), presença em bancos de diásporos, tipo

de dispersão, facilidade na recolonização e grau de crescimento.
Este parâmetro ligado à população, deverá sempre ser tratado tendo em consideração os diferentes parâmetros ligados ao tipo de habitat, como seja o seu tamanho, durabilidade, estabilidade e padrão de ocupação.

Palavras chave: Briófitos, Listas Vermelhas, estratégia de vida, habitat.

INTRODUCTION

The aim of Red Listing of bryophytes (and other organisms) is to estimate the risk of extinction within a foreseen future during present or anticipated conditions. Many older Red Listing attempts (e.g. Floravårdskommittén för mossor 1988), and some newer ones (e.g. RYAN 1996) use rarity (few populations and/or small local populations) as the main factor for Red Listing, assuming that the rarer a species is, the more threatened it is. However, many bryophytes occur only in small populations (SÖDERSTRÖM & HERBEN 1997) that are stable over time. Such species are adapted to those small populations and are not threatened unless the conditions change. But if the conditions change they may rapidly become extinct.

Most populations of bryophytes are, in addition, dynamic. This can be due to habitat dynamics or to internal population dynamics. The dynamics of habitats are in most cases obvious. Decaying logs disappear after some years and in order to survive, epixylic species need to disperse to new substrate patches. Populations of bryophytes may also be dynamic on stable substrates, or the changes may be more frequent than the substrate requires due to fluctuation and/or stochasticity in death and recruitment (SÖDERSTRÖM & HERBEN 1997).

The easiest way to start to evaluate the survival ability of a species is to look at the habitat parameters and ask some questions about its dynamics and distribution pattern. To be able to track substrate patterns several life history parameters can be varied. In this paper I will point at a few “problems” with habitats and the effect they may have, and propose a way to evaluate species based on habitat and population parameters.

HABITAT DYNAMICS AND LIFE HISTORY STRATEGIES

What is the dynamic of the substrate? How long a time can a species expect to persist? These are vital questions for evaluation of species survival expectancy.

For very to fairly stable substrates, growth and persistence (and competitive ability) are the important factors. On mires, for example, continuous growth and branching produces and enlarges clumps. Without any external disturbance, these can live “forever”. For species adapted to stable habitats, any habitat destruction is alarming since recolonisation rate is low. These species typically show low reproduction, become dominant (at least locally) and have a low growth rate (i.e. they are perennial stayers *sensu* DURING 1992).

For species on short-lived substrates it is important to be able to find a new patch as often as old ones disappear. The more temporal a habitat is, the more often must a species "move" to a new patch and the more important will reproduction and dispersal be. The optimal dispersal strategy for a species is to track the spatial and temporal dynamic of the habitat and optimize dispersal strategy to fit it. The two most important questions are **when** must it disperse and **where** does a new suitable habitat patch appear (Tab. 1).

Table 1. Survival strategies for species favoured under different habitat dynamic and habitat structure.

		When must a species disperse	
		Frequently	Rarely
Where will new substrate patches re-occur	Same place	Early reproduction, large diaspores	Long-lived, late reproduction, large diaspores
	Other places	Early reproduction, many small diaspores	Long-lived, late and continuous reproduction, small diaspores

The "when" question is of importance for how much a species should allocate resources to growth and to reproduction. For substrate that is very short-lived, such as dung for example, a species must rapidly produce diaspores, while species on, for example, rocks may delay spore production until they are large enough to produce many diaspores (?), or produce fewer at a time but over a longer period. Thus, the lifetime production of spores may be the same.

The "where" question is actually a question of dispersal in time or in space depending on the re-occurrence of substrates. If suitable habitat re-occurs on the same site a useful strategy is to produce a large number of persistent diaspores that can remain dormant until suitable conditions arise again. Large diaspores are favoured since they are both deposited locally and may be better at surviving dormant for a long time. These will go into the diaspore bank. This is the shuttle strategy *sensu* DURING (1992), used by e.g. *Riccia* species on arable fields. Characteristic for this strategy is that the species fluctuate considerably in visible population sizes.

If suitable habitats re-occur elsewhere, species must produce a large number of diaspores suitable for distance dispersal. Since most diaspores are dispersed by wind, small diaspores are favoured.

Thus, in dynamic habitats, reproduction and dispersal factors are among the most important factors for survival. In order to estimate survival ability we must look carefully into these parameters.

REPRODUCTION AND DISPERSAL

Dispersal (in its widest sense) includes production of diaspores, transport, and establishment. Diaspore production depends to a large extent on the reproductive system. Monoicous species produce spores more often than dioicous ones and it has been shown several times that the proportion of rare plants is higher among dioicous than among monoicous plants (LONGTON 1992, LAAKA-LINDBERG *et al.* 2000). However, the variation is large between species within the same reproductive sytem. The spore production may also vary within species. *Dicranum majus* (a non-threatened species), for example, produces spores frequently and abundantly in central Norway but fails to produce spores in several places in southern Norway (SAGMO SOLLI *et al.* 2000).

Diaspore transport can be split into 3 phases, liberation, transport and deposition. Since most spores are wind dispersed, it is important that the spores are produced in a place where the wind will reach and catch them. Otherwise they will just be local units, irrespective of the size of the spores. There are several strategies for spore release that increase the probability of being caught, e.g. the "exploding" capsules of *Sphagnum* sp. or the "pepper-pots" of *Polytrichum* sp.

Transport *per se* is important. When reaching higher air masses, drought, low temperatures and UV radiation may be a problem (VAN ZANTEN 1977). However, this is probably only important over longer distances than we are usually concerned about for conservation.

Deposition may be a great problem. Since the dispersal is passive, we can expect spores be deposited evenly over the habitat, or collected on the leeward side of any objects. Since the substrate is patchy, a lot of diaspores land on substrate patches that are not suitable for growth. An estimate for *Ptilidium pulcherrimum* (SÖDERSTRÖM & HERBEN 1997) shows that less than 1 % of the produced spores are deposited on suitable substrate outside the immediate vicinity of the colony. This figure is for short-distance dispersal within a good locality and the figure is certainly much lower for dispersal between localities. The more infrequent a substrate is, the more diaspores need to be produced to ensure that at least some are deposited at a suitable locality, unless a special "tracking strategy" is developed (as in the insect-dispersed spores of *Splachnum* species, for example).

It is shown that establishment in the wild may be a problem. MILES & LONGTON (1990) showed that *Polytrichum* sp. did not germinate much in the field although spores were viable. However, HASSEL & SÖDERSTRÖM (1999) showed that on a newly created road, *Pogonatum dentatum* did germinate freely. Research on establishment conditions and frequency is among the most wanted research in population biology of bryophytes.

EVALUATION OF SURVIVAL ABILITY

To be able to evaluate the survival ability of a species one must thus first evaluate the substrate dynamics before one can estimate the possibility to cope with it. Then the species population parameters must be evaluated. I propose the following steps to be taken.

1. Is the substrate stable over time?
   - Yes. Go to step 2.
   - No. Go to step 4.

2. Is there a threat to the habitat that will decrease the habitat area and/or quality?
   - Yes. May be threatened depending on severity of habitat decline.
   - No. Go to step 3.

3. Is the species rare (i.e. with few and/or small populations)?
   - Yes. May be threatened as it is sensitive to stochastic events or may disappear quickly if conditions change. Use the "D" criterion of the IUCN categories (IUCN 1994).
   - No. Least concern.

4. Do conditions re-appear regularly on the same spot?
   - Yes. Go to step 5.
   - No. Go to step 6.

5. Does the species produce diaspores capable of being stored viably in a diaspore bank?
   - Yes. Not threatened unless conditions change (e.g. habitat loss). Rarer species may be threatened using the "D" criterion (few localities).
   - No. Strong candidate for threatened since present reproduction does not match habitat dynamics. Long-term decrease is expected even if habitat does not change. The more temporal substrates are, the faster will populations decline.

6. Do the species produce diaspores in enough quantity? Are they small enough to be expected to disperse by wind over distances? Are they produced in a position where wind can catch them?
   - Yes. Go to step 7.
   - No. Strong candidate for threatened since present reproduction does not match habitat dynamics. Long-term decrease is expected even if habitat does not change.

7. Are establishment conditions on newly available patches suitable?
   - Yes. Go to step 8.
   - No. Probably decreasing since new recruitment is low. May be threatened.

8. Does the species germinate and establish frequently when conditions are right?
   Yes. Least concern
   No. Probably decreasing since new recruitment is low. May be threatened.

Some of the steps above require explanation.

Step 6. It is difficult to evaluate whether a species produces "enough" diaspores that are small "enough" to disperse. However, if reproduction is very rare, and the substrate short-lived, one may expect that reproduction limits its survival ability.

Step 7. Basic research on establishment requirements is needed. Even if conditions are good for mature gametophores to grow, the germination and establishment may be poor. The early stages are often more sensitive to drought and competition than the mature gemetophore stages.

Step 8. Difficult due to lack of basic knowledge of establishment biology. Germinability tests of spores should at least indicate if a species is alive after a time simulating dispersal time and conditions (cf. e.g. VAN ZANTEN 1978, DALEN & SÖDERSTRÖM 1999). Some species may stay alive for years (DURING 1986) while e.g. some tropical epiphytes must germinate within a few hours of spore release (FULFORD 1951).

CONCLUSION

It is of utmost importance when evaluating survival ability of a species to do so in relation to habitat dynamics and population ecology. The final question is if one can expect a species to decrease and be at risk of extinction because the population biology does not match the dynamics of the habitat.

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