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Recommendations for the use of critical terms when applying IUCN red-listing criteria to bryophytes

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The IUCN Red List is recognised as a robust system for assessing the risk of extinction to organisms, but there are difficulties in applying the criteria to bryophytes and other clonal and colonial organisms. Three critical terms are addressed – generation length, mature individual and severe fragmentation – and definitions given in order to facilitate the use of the IUCN Red List criteria for bryophytes. These recommendations provide a pragmatic and effective way of using the IUCN Red List process for bryophytes and may have a wider application to other clonal organisms.

Keywords: bryophytes, clonal organisms, generation length, individual-equivalent, IUCN Red List, mature individual, severe fragmentation

The IUCN Red List of threatened species is widely recognised as an objective system to assess the extinction risk of animals, plants and fungi, as a global indicator of the threats to biodiversity and as an authoritative tool to catalyse conservation actions (Rodrigues et al. 2006, Mace et al. 2008). To date, Red Lists according to the red-listing system of IUCN (2012a) have been established for many different taxonomic groups at various geographical scales (<www.iucnredlist.org>) although they were originally designed for application at the global level (IUCN 2012b). According to the IUCN red-listing system, species are grouped into one of the following nine categories: Extinct [EX], Extinct in the Wild [EW], Critically Endangered [CR], Endangered [EN], Vulnerable [VU], Near Threatened [NT], Least Concern [LC], Data Deficient [DD] and Not Evaluated [NE]. The Red List categories CR, EN and VU, collectively referred to as 'threat categories', are assigned to species (or subspecies or varieties in certain cases) on the basis of five quantitative criteria (IUCN 2012b) that have been developed to estimate the extinction risk to each species assessed. Guidelines for the application of these criteria are regularly updated (IUCN SPSC 2017).

Information on population size, range and trend, number of locations, decline, habitat quality and threats are all needed to apply the criteria. In each criterion, quantitative thresholds are provided for each threat category (IUCN 2012a). Wherever possible, actual data are used, but because of the complex nature of species and their relationships to each other and to their environment, it is often necessary to use inference and projection. A number of terms and concepts are necessary in order to reach conclusions about the various factors employed in the criteria, notably 'mature individuals', 'generation length' and 'severe fragmentation'.

The criteria were developed with the aim of achieving consistency across taxonomic groups, but they are most readily applied to large organisms with clearly identifiable sexually reproducing individuals. For other organisms, however, a Red List assessment based on the IUCN Red List criteria may be challenging. There are several reasons for this, including sheer species numbers, lack of experts, limited availability or poor quality of quantitative data, the life histories of the evaluated taxa and, obviously, combinations of all these (González-Mancebo et al. 2012, Régnier et al. 2015, Willis et al. 2017). IUCN recognises these difficulties and collaborates with the Species Specialist Groups of the IUCN Species Survival Committee to provide detailed Guidelines to encourage consistent application of the Red List criteria across different sorts of organism (IUCN SPSC 2017).

Here we deal with the application of IUCN Red List categories and criteria to bryophytes. Bryophytes are small non-vascular plants that reproduce both sexually and asexually, although at various frequencies depending on species and to some degree on environment (Vanderpoorten and Goffinet 2009). Many populations and even some species do not reproduce sexually, or do so only very rarely, during their entire lifespan (Longton 1997, Bisang and Hedenäs 2005). Most bryophyte species show a continuous apical growth, decay basally, and branch into often numerous ramets which may eventually cover a large area (Glime 2017). Bryophytes can have exceptionally long life-spans, probably reaching hundreds or even thousands of years (Roads et al. 2014), because of these clonal growth patterns. This makes the definitions of 'mature individuals' and 'generation length', two key parameters in the IUCN red-listing criteria, very challenging for bryophytes. Hallingbäck et al. (1998, 2000) have addressed these and other critical issues for bryophyte red-listing, and the results of this work have been applied in red-listing bryophytes at the national level (Hallingbäck 2007).

During the preparation of the European Bryophyte Red List, which is due for publication in 2019 (Hodgetts et al. unpubl.), it became apparent that a revision of the critical parameters would greatly benefit the project and ensure a consistent application of the IUCN criteria by all of the Red List assessors. Therefore, building on the work of Hallingbäck et al. (1998, 2000) and Hallingbäck (2007), this paper presents refined and largely pragmatic definitions of the critical terms 'generation length', 'mature Individual' and 'severe fragmentation'. Suggestions are also given about which of the five IUCN red-listing criteria and sub-criteria may realistically be applied to bryophytes. This approach has been successfully applied in the assessment of the 1800 European bryophytes, and has been circulated to members of the IUCN SSC Bryophyte Specialist Group. We believe that the approach developed for bryophytes may also be useful in red-listing other clonal organisms.

Definition of critical terms

Generation length

Generation length is notoriously difficult to estimate in perennial plants, including bryophytes. IUCN (2012a) defines generation length as 'the average age of parents of the current cohort (i.e. new born individuals in the population)'. The Red List Guidelines (IUCN SPSC 2017) present several different methods for the estimation of generation length, and clonal organisms are addressed specifically: 'for partially clonal taxa, generation length should be averaged over asexually and sexually reproducing individuals in the population, weighted according to their relative frequency' (IUCN SPSC 2017, p. 28). However, for the estimation of generation length according to these guidelines, knowledge on the age of first reproduction, the length of the reproductive period or adult mortality is required. These parameters are virtually unknown for most bryophytes and it is thus not feasible to apply any of these methods.

For practical reasons and consistency, the system for estimating the generation lengths of bryophytes adopted in the Swedish bryophyte Red List (Hallingbäck 2007) has been followed for the European Bryophyte Red List. This closely follows the guidelines for the application of the IUCN Red List criteria for bryophytes published by Hallingbäck et al. (1998, 2000), and is based on the life strategies system for bryophytes developed by During (1979, 1992; Table 1, including specific examples for each life strategies). Based on these life strategies, we used the following pragmatic generation lengths for the European Bryophyte Red List (for examples, see Fig. 1):

- Short-lived species (ephemeral colonists, fugitives, annual shuttles): generation length = 1–5 years; 3 generations = 10 years.
- Medium-lived species (colonists, short-lived shuttles): generation length = 6–10 years; 3 generations = 20 years.
- Long-lived species (perennial stayers, long-lived shuttles, dominants): generation length = 11–25 years; 3 generations = 50 years.
- For species that are never or only very rarely found with sporophytes, and for which also no distinct means of asexual reproduction are known, a generation length of 33 years is recommended; 3 generations = 100 years. There are relatively few species in this category (e.g. *Herbertus* spp., *Pleurozia purpurea*).

Dierssen (2001) published a table of life strategies covering most European bryophytes. For species not included, a bryologist is usually able to assign a life strategy to a species when the basic life history of that species is known. In many cases the life strategy can also be deduced from the species' substrate preferences, the rate of turnover of its habitat, or its spore size (Vanderpoorten and Goffinet 2009). For example, epiphyllous species growing on evergreen leaves are necessarily short-lived, as each leaf lives only for a short time. Most specialist epiphyllous species are short-lived shuttle species (Bates 2009). Knowledge of the phylogenetic relationships of a species can also be useful in determining its life strategy.

What is a 'mature individual'?

The Red List Guidelines (IUCN SPSC 2017) define the number of mature individuals as 'the number of individuals known, estimated or inferred to be capable of reproduction'. Still viable spores in a diaspore bank, protonomata or juvenile individuals currently not capable of producing any diaspores are thus not counted. The Guidelines further recognise that a 'mature individual' may be difficult to delineate in clonal organisms, including bryophytes, and provide the following recommendation (IUCN SPSC 2017; p. 25): 'as a general rule the ramet, i.e. the smallest entity capable of both independent survival and (sexual or asexual) reproduction should be considered a 'mature individual''. In bryophytes, single ramets may reproduce asexually, and even sexually in the case of monoicous species (Haig 2016). Indeed, even single cells have the potential to generate into new plants (totipotency). IUCN SPSC (2017) further states that 'in defining a mature individual for colonial organisms

Table 1. Life strategy system according to During (1979, 1992; slightly adapted) used as a basis for the estimation of generation length. Nomenclature in Table 1 and the figures follows Hodgetts 2015.

Potential life span (years)	Spores numerous, very light (<20 μm)	Spores few, large (>20 μm)	Reproductive effort
<1	Fugitives (*Funaria hygrometrica*, *Diphyscium foliosum*)	Annual shuttles (*Ephemerum cohaerens*, *Tortula truncata*)	High
Few	Ephemeral colonists (*Bryum klinggraeffi*), Colonists (colonists s.str. and pioneers: *Dicranella heteromalla*, *Lophocolea heterophylla*)	Short-lived shuttles (*Ulota* spp., *Exormotheca pustulosa*)	Medium
Many	Perennial stayers (*Brachythecium rutabulum*, *Ctenidium molluscum*)	Long-lived shuttles (*Hedwigia ciliata*), Dominants (*Sphagnum* spp.)	Low

[such as bryophytes], it is important to identify entities that are comparable in demographic stochasticity and extinction proneness to a population of discrete individuals or animals'. Single bryophyte ramets are not likely to compare to these entities.

For some bryophytes (the minority) it may be possible to identify 'mature individuals' as suggested in the Red List Guidelines (IUCN SPSC 2017) for unitary organisms. For example, if a species forms isolated, discrete cushions, as occasionally happens in some mosses (e.g. *Ulota* spp., *Grimmia* spp.), or grows in discrete rosettes as in some liverworts (e.g. *Riccia* spp.) or occasionally in hornworts, it may be possible to treat each cushion or rosette as a 'mature individual' (Fig. 2). However, these species may also grow in less discrete units making it impossible to count cushions or rosettes. Generally, defining what constitutes a 'mature individual' in bryophytes is usually much less straightforward as many species grow in carpets or mats.

In line with the IUCN SPSC (2017) recommendation to 'assume an average area occupied by a mature individual and estimate the number of mature individuals from the area covered by the taxon', the Swedish Red List Committee for Bryophytes interpreted 'mature individual' in a pragmatic way by using the concept of an 'individual-equivalent' (Hallingbäck 2007). This is closely related to the concept of the 'functional individual' in fungal species (Dahlberg and Mueller 2011). Thus, in the European Bryophyte Red List, we applied the following definitions:

- Terricolous taxa growing on the ground on various substrates (sand, gravel, earth, litter etc.), or saxicolous taxa growing on cliffs or on other more or less flat surfaces: an 'individual-equivalent' = 1 m² [i.e. 1 m² in which the taxon occurs, whether as a single ramet or as a dense carpet of many ramets covering most of the surface (Fig. 3)].
- Saxicolous or terricolous taxa on boulders (the latter for example in earth-filled fissures): 'an individual-equivalent' = 1 boulder on which the taxon is growing.
- Epiphytic and epiphyllic taxa: 'an individual-equivalent' = 1 tree or 1 shrub on which the taxon is growing.
- Epixylic taxa: 'an individual-equivalent' = 1 log on which the taxon in growing.

The definitions of 'individual-equivalents' as outlined above closely follow the Red List Guidelines (IUCN SPSC 2017), but they are more precise and also more explicit than those originally suggested by Hallingbäck (2007). They are used in all cases where identification of 'mature individuals' is not possible. For the European Bryophyte Red List, each individual Red List assessment of a species

Figure 1. Examples of species with different generation lengths. Species from top left to down right: *Funaria hygrometrica* (fugitive), *Tortula truncata* (annual shuttle), *Riccia glauca* (annual shuttle), *Lophocolea heterophylla* (pioneer colonist), *Ulota bruchii* (short-lived shuttle), *Exormotheca pustulosa* (short-lived shuttle), *Brachythecium rutabulum* (perennial stayer), *Hedwigia ciliata* (long-lived shuttle), *Sphagnum capillifolium* (dominant; photos: A. Bergamini).

Figure 2. When species grow in discrete cushions such as *Grimmia orbicularis* (left) or as single rosettes (*Riccia* spp., right), individuals rather than 'individual-equivalents' may be counted (photos: A. Bergamini).

consistently specifies how the number of individuals was estimated when calculating population decline: 1) individuals in the strict IUCN sense, or 2) individual-equivalents as described above.

The full rationale for using 'individual-equivalents' is as follows:

1. 'Individual-equivalents' are exposed to extinction risks comparable to those affecting mature individuals of sexually reproducing animals. Examples of threats to 'individual-equivalents' are the felling of a tree, the removal of a boulder, the widening of a road, disturbance by trampling, climbing or by cross-country vehicles, or constructions that affect shorelines.
2. The definitions of 'individual-equivalents' allow realistic estimations of population size and to communicate them in a clear way. They often do not correspond to individuals in a biological sense (see also Dahlberg and Mueller 2011), but they do facilitate the estimation and reporting of extinction risks and the monitoring of population sizes in practical conservation work.
3. 'Individual-equivalents' are comparable to the 'population size units' agreed for use in Article 17 reporting for bryophytes in Annex II of the European Union Habitats Directive (i.e. area covered by population in m^2, number of inhabited logs, number of inhabited stones; see Table 22 in DG Environment 2017).
4. The use of 1 m^2 in the definitions of 'individual-equivalents' rather than smaller units (e.g. 1×1 cm), or using different estimates for different species, avoids many borderline cases and excessive discussions that would obstruct the purpose of using population size as a factor to assess extinction risk.
5. These delimitations of individual-equivalents are in agreement with the latest IUCN guidelines (IUCN SPSC 2017).

Severely fragmented

If most of a taxon's individuals are found in small and relatively isolated subpopulations, these small subpopulations have a reduced probability to re-establish after extinction and the taxon's population may thus be considered 'severely fragmented' (IUCN 2012a). However, the Red List Guidelines (IUCN SPSC 2017) explicitly state that 'the same degree of habitat fragmentation may not lead to the same degree of population fragmentation for species with different levels of mobility'. Even species with an identical spatial distribution may thus experience different levels of population fragmentation. Wide disjunctions are a natural feature of bryophyte distributions (Shaw et al. 2003, Patiño and Vanderpoorten 2018). Many species possess efficient dispersal mechanisms via small spores (usually <20–25 µm; During 1992, Lönnell et al. 2014; but see also Zanatta et al. 2016), and tend to occur in distinct 'microhabitats' within different 'macrohabitats' in different geographical regions. Yet, empirical evidence of the effects of habitat fragmentation on bryophyte species populations is ambiguous (Lönnell et al. 2014, Kiebacher et al. 2017, Löbel et al. 2018). Whether a disjunct distribution of a species implies 'severe fragmentation' needs therefore to be considered in the light of a range of factors

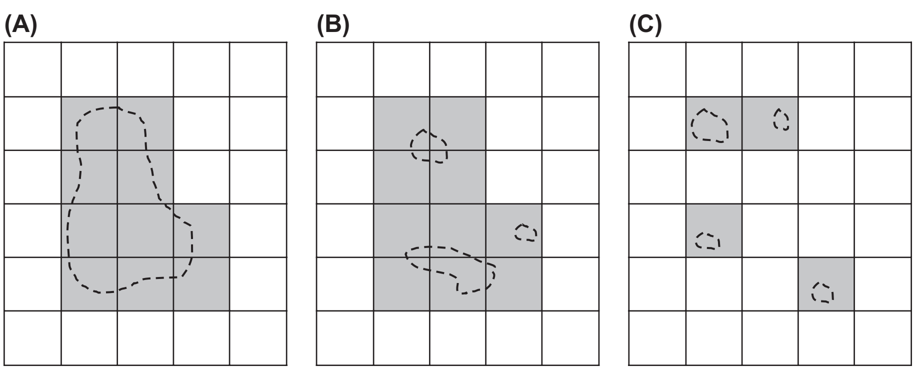

Figure 3. The use of 1 m^2-squares in defining 'individual-equivalents'. All occupied squares are counted, resulting in ten 'individual-equivalents' in A and B, and four in C. Dashed lines: patches of the species; grey squares: occupied 1-m^2-squares.

such as its natural rarity, the frequency and potential of its reproduction, both sexual and asexual (including ramet fragmentation), its diaspore size, the nature of the landscape in which it occurs, and its habitat. It is crucial that all available data and expertise are taken into account for each individual species. When evaluating whether a species is 'severely fragmented', we recommend to compare the species' life strategy (During 1979, 1992; Table 1) with the species' distribution and habitat. A colonist species that happens to occur in a few widely scattered localities would probably not be considered 'severely fragmented' unless the habitat itself is rare or has become fragmented. On the other hand, species which produce rather large spores (usually >20–25 µm), such as the short- to long-lived shuttle species, and which occur in specific rare and fragmented habitats, would be considered 'severely fragmented'. Note that the threshold values of spore sizes given above are approximations. There is evidence that also larger spores enable trans- or intercontinental dispersal; for example in *Sphganum* species (Sundberg 2013) where spores are actively discharged up to 20 cm above the capsule (Whitaker and Edwards 2010). The decision on whether a particular species is 'severely fragmented' has to be made on a case-by-case basis, and includes to some extent subjective judgement.

This recommendation closely follows Hallingbäck et al. (1998, 2000), though without providing specific distances or thresholds indicating fragmentation.

Consequences of the refined definitions on the application of the IUCN criteria

The definitions of the three critical parameters addressed above affect at least four of the five IUCN Red List criteria: generation length is required for the application of criterion A (reduction in population size); population fragmentation for the application of criterion B (geographical range); and the number of mature individuals for both criteria C and D (both of which consider population size).

The new definitions of generation length and severe fragmentation closely follow previous guidelines for the application of IUCN red-listing methodology to bryophytes (Hallingbäck et al. 1998, 2000) and will therefore hardly affect assessments. The pragmatic definition of 'mature individuals' as 'individual-equivalents', however, will have a greater impact, possibly leading to a more frequent use of criteria C and D. In many previous Red Lists, criterion C was only rarely used or not used at all. Of criterion D, only D2, which does not require information on the number of mature individuals, was frequently applied (e.g. Switzerland; Schnyder et al. 2004). So far, authors of bryophyte Red Lists from various parts of the world generally considered numbers of 'mature individuals' to be too high to meet the thresholds of these criteria (Baudraz, Bisang, Bergamini, unpubl.). With the new, more pragmatic use of 'individual-equivalents', the use of criteria C and D is more feasible. For example, the total number of trees occupied by a species may be known or inferred, whereas the number of individual patches or ramets of that species would be virtually impossible to estimate.

Despite the new definitions of the critical terms, the major problems for applying the IUCN criteria for bryophyte red-listing will largely remain the same: poor data quality (e.g. lack of precise locality information, no recent data), limited accessibility of data since locality information is not digitized, and huge data-poor regions because of a general lack of bryologists especially in tropical regions (von Konrat et al. 2010, Geffert et al. 2013). Nevertheless, even when quantitative, high quality data are lacking, the criteria may still be applicable (IUCN SPSC 2017). For example, population reductions can be inferred or suspected based on changes in habitat quality (IUCN SPSC 2017). We strongly recommend that bryologists who are struggling with Red List assessments contact the Steering Committee of the IUCN Bryophyte Specialist Group (AB, IB and JvR) or the authors of this paper for advice.

Outlook

The definitions of critical terms presented here have already been successfully applied in the Red List assessment of European bryophytes. They were subsequently circulated among members of the IUCN SSC Bryophyte Specialist Group. The Steering Group of the IUCN Bryophyte Specialist Group will propose to its members to use these definitions of critical terms in future global Red List assessments. This publication of the refined critical terms will also help to promote their use for regional or national Red Lists, as is currently the case for the revision of the Red List of threatened Bryophytes of Switzerland. We believe that if the definitions of critical terms provided here are widely used, they will further increase consistency of assessments among regions and assessors. Furthermore, the definitions described here may be relevant for red-listing in other clonal organisms (corals, lichens, algae, vascular plants).

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