England's Rare Mosses & Liverworts

Their history, ecology and conservation

Ron D. Porley

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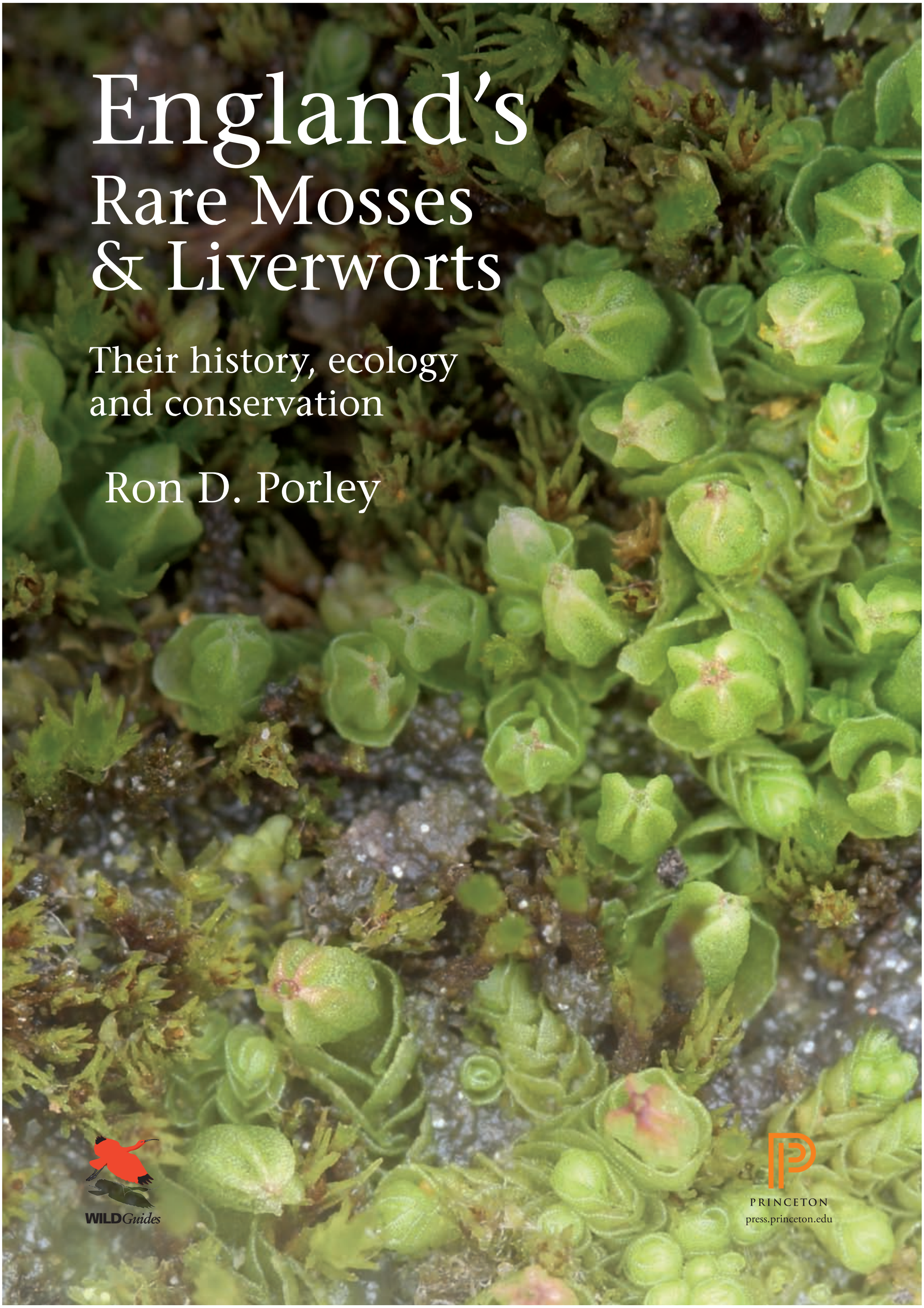

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COVER: *Fissidens serrulatus*, a Mediterranean–Atlantic moss of shady riverbanks known from two localities in Cornwall and Devon. Photo: Ron Porley.

FRONTISPIECE: The Vulnerable dioicous liverwort *Solenostoma caespiticium* with male (*right*) and female (5-winged perianths) plants. Photo: Štěpán Koval (Czech Republic).

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Introduction

Man is placed in the middle between two infinities – the infinitely great and the infinitely small – both of which are incomprehensible to him.
Edinburgh Encyclopaedia

This is a book about mosses and liverworts, collectively known as bryophytes, a term derived from ancient Greek and first used around 1878. Britain is currently home to 1,044 species, comprising 752 mosses and 292 liverworts (1,048 if the four British hornworts are included). They are small, relatively simple plants that live on the land (although some have returned to freshwater), and depend upon water for fertilization. They are the earliest known land plants and were thriving on the ancient landmasses of Pangaea and Gondwana-land millions of years before flowering plants made their entrance onto the world's evolutionary stage. As a result of their small stature, they have been able to exploit a diverse range of niches of which many are unavailable to so-called higher or flowering plants. They are supremely adapted to life on earth, not least because of their ability to remain alive for long periods of time without water and yet rapidly recover when wetted with rain or dew.

In England, there are 666 mosses and 252 liverwort species (excluding four hornworts). Some 87 (9%) are on the revised Red List of British bryophytes, a system that estimates the extinction probability if nothing is done to change the situation. A total of 84 species of English threatened bryophytes is profiled in this book, and a further three species have not been seen in England for more than 50 years. But this is not a Red Data Book *per se*. Instead, the emphasis is on understanding rarity, what causes it and the implications for conservation. Rarity is a complex notion, yet we think we know what it means and use the term in everyday conversation. Many bryophytes are naturally rare and flourish, but many more have had rarity thrust upon them by human activities. If conservation can reasonably avert the extinction of a bryophyte, and the understanding gained thus helps safeguard other populations, then morally it is right that we do so. The key to preventing a plant sliding inexorably towards possible extinction is an awareness of what leads to a species becoming rare in the first place. This book brings together the relevant literature to understand what 'rare' means in the context of mosses and liverworts. In doing so the intention is not to elevate the importance of the rare at the expense of the common. Arguably the common species are more important in the wider picture; paradoxically a common species may be more threatened if it occupies an environment that is decreasing or if it has a life-history that depends on the maintenance of large or numerous populations. Bryophyte conservation and recording is not just about the plants; it is about people too, past and present, who have done so much to propel England (and Britain) into the position of one of the best bryologically known countries in the world. Their contributions are acknowledged throughout the book.

England is one of the mostly densely populated countries in Europe, with 395 people per square kilometre, constituting 84% of the total United Kingdom population. The most densely populated areas of England are the major cities and metropolitan areas of London and the South East, South and West Yorkshire, Greater Manchester and Merseyside, the West Midlands and the conurbations

It could be argued that many bryophytes were lost from these areas long ago, and that now the battleground has shifted to areas of the country that have been spared the ravages of the Industrial Age such as the south-west of England (although tin mining had a long and productive history here and has given rise to important bryophyte habitats) and ostensibly protected areas, for instance the New Forest in Hampshire.

Wales and Scotland (for the latter see Rothero, 2005) also have a fair measure of threatened bryophytes but many of their rare and interesting species occur in more remote and relatively undisturbed habitats; there is greater pressure on lowland habitats and species further south in Britain. No part of Britain is, however, free from the pervasive effects of pollution, nutrient enrichment and climate change. Species action is often funded under UK or European initiatives, and then is normally implemented at the national level. The statutory conservation agency Natural England (*NE*) is the body tasked with ensuring that biodiversity, including bryophytes, is not eroded in England.

Bryophytes are no respecters of national frontiers. In a phytogeographical context England is part of the British Isles and the wider Atlantic Biogeographic Region which encompasses the UK, Ireland, and the western parts of Denmark, Germany, The Netherlands, northern Belgium, north-west France, the northern shores of Spain and a small area in the north of Portugal. This is a key concept in the EC Habitats Directive, a powerful European Union (EU) instrument, where sites for the protection of habitats listed at Annex I and species listed at Annex II of the Directive are selected in the context of such Regions. Site protection and habitat conservation are vital, if not the most effective mechanism available, to maintain and increase populations of bryophytes. This topic is covered in the section on 'Conservation measures' (*page 19*). The 'listing' of species and habitats is seen by some as an activity that is interminable, sometimes excessive and to the more cynical to keep bureaucrats in a job, but it is genuinely fundamental to any conservation programme. It provides not only an inventory of what species occur in any geographical area but guides the allocation of scarce conservation resources. Furthermore, lists are used extensively in enforcement and legislation, themes also covered in the section on 'Conservation measures' (*page 19*).

The species profiled in this book are English bryophytes drawn from the revised Red List of British bryophytes (Hodgetts, 2011). The Red List uses criteria and categories developed by the International Union for Conservation of Nature (IUCN) to determine which species are most threatened and hence in need of conservation action (see *page 31*). It is possible to apply the IUCN system at any geographical scale, but whether this would be sensible for a land the size of England is debatable. If the IUCN criteria were applied to England alone the list would be quite different. There are many bryophytes that would be regarded as rare in the English context if localities or populations were counted, but just across the border the same species may be frequent or even abundant. The wisdom of channelling finite resources into protecting such species is open to question. England has a very effective network of Wildlife Trusts that focus action at the county level and this is commendable since local extinctions can reverberate wider. Thus, although this book focuses on England's rare and threatened bryophytes derived from the British Red List, it provides pointers to conservation priorities at all levels.

Bryologically, the British Isles is one of the best mapped regions, with 'dot maps' that are envied across the world. Yet at the other end of the scale, at the site level, we are not so good. Conservation often falters because those who implement action on the ground are frequently unaware that a particular species is present. Regrettably, the lack of awareness of what species occurs on which site hinders progress in the conservation of England's bryophytes. It is an uncomfortable truth that simple neglect or the accidental obliteration of a bryophyte through ignorance is also a threat.

The consequences of *over*-collecting in the past cannot be denied and examples of where unrestrained collecting has arguably caused a significant decline of a species are mentioned in the relevant species profiles. Although the bryologist of today is more conservation conscious and acts responsibly, populations of rare bryophytes, even on designated sites, continue to be at risk because their presence is not known or known to only a few. In this book it was judged important to be as transparent as possible about sites where threatened bryophytes are known to occur.

A principal aim of this book is to make this particular group of plants and their conservation needs more accessible to a wider audience, through the eye of many skilled photographers, with images of the mosses and liverworts that in all their diversity are sadly at risk of extinction in England if we allow it to happen. Images are powerful: it is much easier to empathize with the loss of something precious if you have a picture of it in your mind. We are rightly concerned about the plight of the European Lynx. Most people have never seen one in the wild but nevertheless know what a lynx looks like because they have seen pictures of it in books, on the internet or on television. It is not to suggest that *Leiocolea rutheana* or *Timmia megapolitana* will ever be as iconic as charismatic megafauna but at least it is hoped that this book will enable readers to appreciate their beauty and be inspired to care for these and other threatened bryophytes.

The images are almost all digital and have been provided by many people; in terms of provenance most are from Britain (all the habitat pictures are), but several are from Europe and a couple are from North America. A bryophyte from the European mainland, or indeed from across the Atlantic, looks much the same as its English equivalent so the priority has been to select the best picture available to give a true likeness of the species. Photographs of bryophytes growing in the field are used wherever possible but for two species no images could be traced. *Lophozia herzogiana* is depicted by an illustration from Jean Paton's 1999 *British liverwort flora of the British Isles* and *Acaulon mediterraneum* is taken from volume 3 of *Flora Briofítica Ibérica*, 2006.

What are bryophytes and why are they important?

Small is beautiful

A bryophyte is a land plant with enclosed reproductive structures that does not have highly developed vascular tissues (for the internal transport of water and nutrients). Neither does the plant have a flower or produce seeds, reproducing as it does sexually via spores and/or asexually by a range of propagules. Such a definition scarcely does justice to the beauty of these small humble plants that adorn our world. The exquisite lithographic prints by Ernst Haeckel (1904), illustrating the remarkable diversity of form of mosses (*left*) and liverworts speaks to us much more lucidly than words can. Although the term 'bryophyte' is used throughout this book to refer to mosses, liverworts and hornworts as a group, it really refers to a shared structure and way of life rather than a group with a single evolutionary origin; indeed all three groups evolved separately from one another and from other plants albeit from a green algal ancestor (see below).

Mosses are perhaps the most familiar group. Typically they have green leafy shoots, either as upright shoots or straggling over the ground. The leaves are spirally arranged on the stem although on occasions may appear flattened in one plane, and often (but not always) have a nerve or mid-rib down the centre of the leaf. Mosses have traditionally been separated into two main types: acrocarps which are typically erect and mostly unbranched and pleurocarps which are prostrate and highly branched. The spore-producing structure, the sporophyte, is attached to the leafy plant, and the spore-containing capsule is held aloft on a thin stalk (seta) or sometimes inconspicuously hidden amongst leaves. The mouth of the capsule may or may not have a ring of teeth, the peristome, which helps to regulate the release of spores. If a plant has sporophytes it is often referred to as 'fruiting', a throwback to an earlier century when it was thought the moss capsule contained seeds.

Leafy **liverworts** are generally softer plants, with leaves arranged along the sides of a weak stem, and the sporophyte is almost evanescent, comprising a translucent stalk and a dark shiny spherical capsule. Spores are released by rupture of the capsule wall. The thalloid liverworts, lacking leaves, look quite different and appear as tiny rosettes to moderately sized mats of green tissue, sometimes resembling certain lichens. Whilst thallose lichens are usually of a different often paler colour on their underside and are relatively tough, thalloid liverworts are similarly green on both sides and the texture is soft and rather delicate.

Hornworts, the third bryophyte group most closely resemble the thalloid liverworts but have quite different long-lived sporophytes that resemble tapering horns, splitting along their length to release the spores. None of the four British species of hornworts are currently on the revised British Red List although one, *Phaeoceros carolinianus*, was previously considered Endangered but recent survey has found no evidence of a decline and it has been downgraded to Near Threatened. Therefore, hornworts are not considered further in this book.

There are many other morphological differences (as well as similarities) between the three lineages of bryophytes, and the reader should consult other works for more detail on this topic (see Porley & Hodgetts, 2005; Schofield, 1985; Vanderpoorten & Goffinet, 2009).

A print from Ernst Haeckel's 1904 *Kunstformen der Natur* celebrating the astonishing diversity of form in mosses.

Alternation of generations

A common feature amongst the bryophytes is the phenomena known as alternation of generations, discovered by Hofmeister in 1851. This life cycle, where a dominant haploid branched gametophyte (the green leafy plant) alternates with a diploid unbranched sporophyte (the spore producing structure) is unique in living land plants. In most other land plants the gametophyte is extremely small; in ferns it is the free-living structure called the prothallus (which is often mistaken for a thalloid liverwort in the field!). By contrast, in flowering plants and conifers the gametophyte is reduced to just a few cells (embryo sac and pollen) and is enclosed within the much larger dominant sporophyte phase (for example, the oak tree or the rose plant).

In bryophytes the transition from haploid (the gametophyte with one complete set of chromosomes) to the diploid state (the sporophyte with two complete sets of chromosomes) is brought about by fusion of egg and spermatozoid. The switch back from diploid to haploid is mediated by meiosis, and leads to spore formation. The spore, with one set of chromosomes, ultimately gives rise to the green plant (gametophyte) we recognize as the moss, liverwort or hornwort and its cells divide and multiply by the process of mitosis. Such a life cycle has predestined bryophytes to a life dependent upon water for a motile spermatozoid (or sperm) to effect fertilization of the egg (some recent work however has suggested sperm dispersal may also be assisted by micro-arthropods such as mites (Cronberg, Natcheva & Hedlund, 2006).

The earliest land plants

The advent of land plants is one of the most important events in the Earth's history. It changed global climates and biochemical processes and set the stage for the evolution of all eukaryotic (organism whose cells contain complex structures enclosed within membranes) terrestrial life on Earth. The first plants that colonized land were probably plants at a bryophyte level of organisation, most likely a liverwort. Thus bryophytes represent the earliest of the land plants. Various strands of evidence indicate that green algae are the ancient forebears of bryophytes and, by implication, all other land plants and that colonization of the land began on the eastern shores of the ancient landmass Gondwana as long ago as the early Palaeozoic, some 543–248 million years ago (Rubinstein *et al*., 2010).

It is difficult to be precise when the first true liverwort, moss or hornwort appeared due to uncertainties in interpreting the fossil record. Astonishingly, a compression fossil found in China dating from the Cambrian Period (about 500 million years ago) is thought to be a possible moss, morphologically close to the extant genus *Funaria*. Nonetheless, by the close of the Palaeozoic era, the main bryophyte evolutionary lines were established. To put this into context, bryophytes were on the Earth some 264 million years *before* the arrival of flowering plants. Today, the flowering plants are the most diverse plant group on the Earth with an estimated 250–300,000 species occurring worldwide. Bryophytes are the second most diverse plant group, at just over 16,000 kinds known to science, yet it has been suggested that the true total may be around 22,000 (Chapman, 2009). A recent estimate of world liverwort species is given as 7,500 (von Konrat *et al*., 2010). The number of molecular studies at the population level in liverworts and mosses is currently limited and thus we have little appreciation of the scale that 'cryptic' species contribute to bryophyte biodiversity; existing studies suggest a significant part of bryophyte biodiversity is undetected with traditional morphological concepts alone (Heinrichs *et al*., 2009).

Small yet successful

Fundamental to understanding why bryophytes have survived for so long and are so successful is their adoption of the poikilohydric life-style, which means their ability to dry out, suspend metabolism and then resume physiological activity when water becomes available, a key step in their evolutionary development. Despite their apparent delicate and fragile appearance bryophytes can withstand extreme changes in water availability. Their water content is directly regulated by the ambient moisture and they are capable of absorbing water over the whole surface of the plant, aided by a multitude of shoot and leaf adaptations (including papillae, lamellae and tomentum) designed to exploit surface tension phenomena. A moss such as *Grimmia* growing on an exposed rock surface can dry out completely and enter a kind of dormancy, then rapidly resume physiological activity come the first raindrops or overnight dewfall. They can do this with no degradation of cell organelles or membrane disruption by virtue of possessing a set of protective proteins, the accumulation of soluble sugars, and metabolic repair mechanisms. Even bryophytes of typically moist environments such as cloud forest can tolerate days of drought more than most flowering plants could survive. Nevertheless, there is great variation in the extent of desiccation that different species of bryophyte can tolerate.

Bryophytes have remained small throughout their evolution chiefly because they have not evolved lignin, a substance giving other land plants rigidity that enables them to grow tall in their struggle to reach the light. It seems that desiccation tolerance is an adaptive strategy for bryophytes *because* they are small (Proctor *et al.*, 2007) and one that has enabled bryophytes to grow in places and under conditions denied to other land plants. It is because bryophytes are so closely tied to the external environment that they represent excellent indicators of climate change (Tuba, Slack & Stark, 2011).

Importance and uses of bryophytes

The ecological importance of bryophytes is belied by their small size. They contribute to a substantial proportion of the global plant biomass in a range of ecosystems, in particular peat bogs, other wetland vegetation and forest systems. They play a major role in carbon and nutrient recycling as they are net sinks of carbon dioxide, particularly in the northern peatlands, regulate water availability by acting as slow release sponges in many forest systems, may promote soil formation facilitating the establishment of other plants, stabilize and protect soils against wind and water erosion, and mediate soil temperature and moisture. On account of these attributes, together with sensitivity to pollution, bryophytes are extensively used as biological indicators in both terrestrial and aquatic environments. Countless invertebrates use them for shelter and egg-laying sites, yet direct consumption by animals is limited owing to a armoury of protective secondary compounds discouraging herbivory.

An excellent review of the uses of bryophytes is provided by Glime (2007). It would be misleading to suggest bryophytes have an economic importance approaching that of flowering plants but they do have their moments. Peatlands, dominated by *Sphagnum* moss, are the source of peat for horticulture, a particularly environmentally damaging but lucrative industry for which alternatives are now being found. Living *Sphagnum* because of its high absorbency and inherent antibacterial properties was also used as a wound dressing during various wars, including World War I, and was collected in large quantities (see *next page*) from Scotland and England. Today it is used for nappies, cleaning up oil spills and filtering

Large quantities of *Sphagnum* moss were collected during the First World War for use as field dressings. Men and women are filling sacks on the bleak hills of Dumfriesshire. (Reproduced by permission of D. Forman).

of industrial and domestic effluents, uses that exploit its superior absorbent properties. Other mosses are increasingly being investigated for waste water treatment and recycling in a range of situations. In Britain, large pleurocarpous mosses were harvested and sold to florists as moisture retentive medium for bulbs. For example, up to the 1970s at Lakenheath in the Brecklands of East Anglia, *Pleurozium schreberi* was raked out of the turf and stuffed into sacks for just this purpose.

One of the earliest documented medicinal uses of bryophytes is in a 16th century *Chinese Compendium for Materia Medica*, and bryophytes are still used in Chinese and native North American's folk medicine today. Increasingly bryophytes are being screened by the pharmacological industry for antibacterial and anticancer activity, and researchers are particularly interested in bryophyte genes that code for desiccation tolerance and substituting these into commercial crop varieties such as tobacco. Various mosses also have an application in construction, such as insulation and fire proofing, still practised to this day in some parts of the world, and more mundane uses including doormats and brooms (using *Polytrichum*). Bryophytes have long been used in various fields of scientific endeavour but have come of age for the evolutionary window that they can provide on understanding land plant development. The genome of *Aphanorrhegma* (*Physcomitrella*) *patens*, a common moss in Britain, was sequenced by an international consortium and published in 2008. The genome is estimated to contain approximately 35,000 genes, or 486 million base pairs, more, surprisingly, than revealed in the sequence of the flowering plant thale cress (*Arabidopsis*) (Cuming, 2011). With regard to genetic engineering, mammalian genes transferred into the moss genome of *Aphanorrhegma* have resulted in the production of mammalian proteins and, in the future, may offer promise for the large scale manufacture of therapeutic proteins such as insulin.

The aesthetic beauty and spiritual fulfilment to be gained from an appreciation of mosses is well known to the Japanese. Moss gardens have existed in Japan since the 14th century; many of them associated with the grounds of Zen Buddhist temples imparting an ambience of great serenity and peace to those who tread within. This reminds us that we do not always need to exploit nature for it to have a value and it is not there simply for our gratification. Bryophytes have a place in this world, if only for their own sake. And we do have a moral obligation to ensure they continue to enrich the world and inspire us.

Rarity in bryophytes

The pressure of a steadily increasing human population on the biodiversity of the planet is an all too familiar theme, bringing with it habitat loss and fragmentation, modification (including the spread of invasive species), over exploitation, pollution and climate change. Closer to home the natural environment in England is much less rich now than 50 years ago (*NE*, 2008). The global, regional and local decline in rare (and common) bryophytes can, in part, be attributed to these factors.

But what is a rare bryophyte? In practice this a difficult question to answer. The first thing to recognize is that of the 1,048 (922 in England) bryophytes known to occur in the British Isles most can be considered as 'rare'. Rabinowitz (1981) proposed what has become the most widely cited classification of rarity. In this scheme, a species is classed as rare if it fits just one of the following criteria: a narrow or highly disjunct geographical range, high habitat specificity, or a consistently low population size. Analysis of the British flora by Birks *et al.* (1998) showed that whilst the majority of species have a large geographical range, about 79% of liverworts and 77% of mosses have high habitat specificity and 80% of liverworts and 81% of mosses have a consistently low population size. This is in line with our knowledge of the biological world in general: that most of the world's plants and animals are rare in some sense of the word (Kunin & Gaston, 1993).

Distribution is just one way of viewing rarity; evolutionary history and genetic variation are equally valid approaches and are, of course, interrelated. This issue is considered in some detail in the section on 'Conservation measures' (*page 19*). In this section, we look at some of the biological characteristics of bryophytes that may lead to them being rare, habitat dynamics, and distinguish natural rarity from human-induced rarity.

Reproductive biology and rarity

To understand at least some of the reasons for rarity in bryophytes we need to consider their reproductive biology. Bryophytes are able to reproduce sexually, producing spores by meiosis following fusion of male and female gametes, or asexually which essentially bypasses any mixing of genetic information (spores and asexual propagules are known collectively as diaspores). Sexual reproduction enables dispersal (via spores) in both time and space and introduces genetic variation, crucial aspects for survival. Spores may be small enough to be carried in wind currents although the actual distance depends on many factors. Spore production may not occur for a number of reasons (including failure to produce antheridia or archegonia) and those species that do not produce spores are significantly rarer than those that do. Finally there is 'clonal reproduction', a form of asexual reproduction, where the disintegration by decay of protonema, stems and other structures leads to separate fragments that can multiply and contribute to the maintenance of the population (Frey & Kürschner, 2011).

Mosses and liverworts have either *separate* male and female shoots (the dioicous state, about 56% of British mosses and 68% liverworts) or the male and female organs (gametangia) are on the *same* shoot (the monoicous state, about 44% of British mosses and 32% liverworts). The monoicous state is traditionally further subdivided depending on the relative position of gametangia on the shoot. About a dozen bryophytes, mostly liverworts, may show both states. In dioicous species, for spore production to occur the male and female shoots must be close enough to facilitate gamete (sperm) transfer and fertilization, typically a few centimetres or less. As a result, a much higher proportion of dioicous bryophytes fail to produce sporophytes (the capsule or spore producing organ). By contrast, monoicous species have the potential of self-fertilization. In the British Isles monoicous mosses are, perhaps unexpectedly, significantly rarer than dioicous species although this pattern is not seen in liverworts. Within the rare monoicous group, mosses and liverworts show differences in terms of sporophyte production; in mosses most species produce sporophytes freely but many rare monoicous liverworts are not known to produce sporophytes at all.

Analysis of the sexuality and rarity in the British bryophyte flora (Longton, 1992; Laaka-Lindberg, Hedderson & Longton, 2000) has shown that most rare bryophytes are either dioicous species that fail to produce sporophytes or monoicous species that commonly produce sporophytes. This suggests that dioicous species become rare because of the failure to produce sporophytes, which limits either their dispersal potential (ability to spread to suitable habitat) or their genetic variation (they become 'less fit' and are thus less able to respond to environmental change). If low genetic diversity could be demonstrated as a causal factor of rarity in dioicous species an effective conservation strategy may be achieved by reciprocal transplantation between male and female populations. Experimental studies have shown that suitable habitat patches may remain unoccupied or 'empty', demonstrating that dispersal related factors is the likely explanation for rarity at least in some bryophytes (Söderström & Herben, 1997).

In monoicous bryophytes, those that fail to produce sporophytes for whatever reason may also suffer the same constraints but, since monoicous bryophytes are more likely to be rare than dioicous species, another explanation is needed. In this case, where the plant is rare but commonly produces sporophytes, one explanation may be that self-fertilization occurs leading to reduced genetic variability and thus the ability to adapt to changing environmental conditions is compromised – akthough there are currently no data to support this hypothesis.

Asexual reproduction

Many British bryophytes, about 46% of liverworts and 17% of mosses, produce some kind of asexual propagule (Laaka-Lindberg, Korpelainen & Pohjamo, 2003). Specialized asexual propagules, such as gemmae, bulbils and tubers (see *pages 16–17*) probably serve mainly as a means of local persistence and enable rapid colonization when conditions become favourable. All bryophytes can potentially regenerate from fragments of leaves, shoots and other parts; this is known as 'totipotency', the ability of a single cell to divide and produce all the differentiated cells in the organism. Dispersal and regeneration of bryophyte fragments is thought to occur quite widely in nature. This mode of dispersal has been little studied in British bryophytes, although regeneration could not be experimentally induced in the Red Listed *Tortula cernua* (*page 183*) using leaf fragments (Headley, 2006). We need to understand better the part played by asexual reproduction in maintaining populations of species that theoretically lack longer distance dispersal capacity. Production of asexual propagules does not seem to have any significant correlation with rarity in mosses or liverworts, although there is an association with spore size and sexuality (see below).

Since specialized asexual propagules are relatively large (compared to spores) it is believed that they are poorly adapted for wind dispersal and, instead, play a role in short distance dispersal (typically in the order of centimetres) and thus are important in maintaining local populations. Most British liverworts that can produce asexual propagules do so much of the time and production is independent of sexuality. Liverworts that produce neither asexual propagules nor spores are the group most likely to be rare. By contrast, dioicous mosses produce asexual propagules much more frequently than monoicous species, and frequent asexual reproduction is found more often than expected among mosses for which sporophytes are unknown and less often in species with sporophytes, particularly so in dioicous species. Production of asexual propagules also shows a strong link to the colonist group of dioicous mosses (see life-history strategies section below).

There is also evidence that asexual reproduction is related to spore size (Söderström & During, 2005). Small-spored species tend to produce asexual propagules more often than expected compared to large-spored species (in general, small spores are ≤25 µm; large spores are ≥25 µm). This trend was not evident for monoicous mosses. Furthermore, in dioicous mosses small spore size is correlated with a short lifespan, while in monoicous mosses species with short-lived shoots and big spores tend to be in the majority.

Life-history strategies

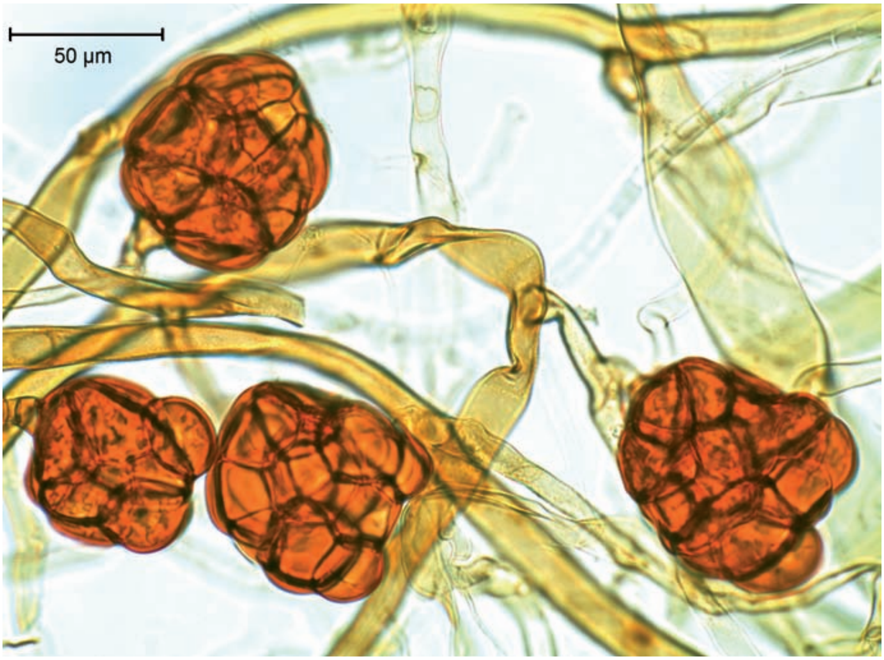
The *concept* of life-history strategies (During, 1992) recognizes different groups of bryophytes based on reproductive effort, spore size and lifespan and how they can survive in a changing environment through a number of 'trade-offs'. A species may invest resources and effort into producing a few large spores, which may have a greater chance of establishment and survival but may not disperse very far, or many small spores that may be able to disperse large distances but may have a reduced establishment and survival probability, or the potential lifespan of the bryophyte may be negatively correlated with reproductive effort. The strategies include perennial stayers that are characteristic of stable habitats and short- and long-lived shuttle species and colonists which typically grow in cyclical temporary habitats. Some bryophytes are capable of exploiting more than one life-history according to their habitat and the prevailing conditions. There is a tendency for colonists and perennials to be dioicous (*Thamnobryum angustifolium* (*page 175*) is a good example of a dioicous perennial moss in which sporophytes are unknown), while annual and short-lived shuttle species are mainly monoicous.

Colonists comprise about 51% of the total British moss flora overall (Longton & Hedderson, 2000), and are typical of habitats available for short periods of time such as arable land. They assure continuity of the population by, for example, the development of tubers on underground rhizoids. Analyses of threatened British bryophytes (Hodgetts, 1996) showed that most short-lived shuttle species were classified as Endangered or Critically Endangered, with relatively few classified as Vulnerable, whilst most perennial stayers are Vulnerable (see section on 'The Red List' (*page 31*) for an explanation of these terms). The high representation of colonists and shuttle species amongst the threatened species has implications for their conservation since these require regular disturbance of the habitat in

Spindle-shaped gemmae borne on shoot tips (pseudopodia) of the moss *Aulacomnium palustre*. Photo: BBS (Iceland).

Disc-shaped gemmae in half-moon gemmae cups on the thalloid liverwort *Lunularia cruciata*. Photo: Ron Porley.

Tiny many-celled bulbils in the axils of the upper leaves of *Pohlia bulbifera*. Photo: Des Callaghan.



Tubers on the rhizoids of *Bryum klinggraeffii*, a common arable field moss. Photo: Rachel Carter.

order to provide favourable conditions. A final word of caution: the analysis of the British bryophyte flora life-history strategies needs much more study. The life-history adopted by an individual for survival is likely influenced by many factors and it will vary across the geographic range of a species; as yet, the allocation of a species to a particular life-history group is often based on theoretical assumptions rather than on direct field data.

Habitat dynamics and rarity

Globally, bryophytes show both broad and highly disjunct distribution patterns. For the last 50 years or so, the approach has been to explain this by the separation of the early supercontinent Pangaea into the southern supercontinent Gondwana and the northern supercontinent Laurasia, which began some 200 million years ago. Bryophytes were rafted far and wide on the fragments and came to rest as the tectonic plates repositioned themselves – the continental drift theory. This may explain many of the broad distribution patterns, but overlain on this is long-distance dispersal by wind. This has long been invoked as a mechanism for dispersal of bryophytes but until recently there had been little experimental support (Muñoz *et al.*, 2004). It is suggested that subsequent regional population extinctions have given rise to some of the disjunct distributions of bryophytes we see today, a view attracting growing support following recent studies based at the molecular level.

There is evidence from palaeoecological studies of fossil bryophytes from the late-glacial/post-glacial transition that mosses and liverworts responded rapidly to major environmental changes (Birks, Heegaard, Birks & Jonsgard, 1998), and that they could migrate and colonize newly created habitats with remarkable speed. Wind the clock forward to the present day amid a modern landscape and it seems reasonable to suggest that there are significant constraints on the ability of bryophytes to effectively disperse and find optimal habitat. Data on fragmentation and habitat losses in England have been presented elsewhere (*NE*, 2008), and only the general principles of habitat dynamics as they relate to bryophyte populations are discussed here.

Metapopulation dynamics and fragmentation

The survival of a bryophyte depends not only on population dynamics within small parcels of habitat known as habitat patches, but on the dynamics between the habitat patches – the so-called metapopulation dynamics. This essentially states that immigration and extinction between patches must be in balance for a species to survive, yet this interplay is determined by the ability of the bryophyte to disperse and the nature of the landscape. If the distance between habitat patches is too large, or barriers too great to overcome, dispersal between them may be reduced or not occur at all. Alternatively, the habitat may be available for a short time only, and the dispersal may be too slow to happen relative to the duration of the patch.

Habitat parameters, including size, quality, spatial and temporal distribution and number of patches, have been much less studied than population dynamics but one of the clearest changes in the modern landscape is that of habitat fragmentation. The resulting decrease in the area of habitats ultimately leads to a decrease in local populations and an increased risk of local extinction; total diaspore production decreases and, most critically, the distance between habitat patches increase such that dispersal distances are greater than before. Indeed, the regional scale distributions of bryophytes are usually limited by habitat dynamics and rather less by population dynamics, a view supported by bryophyte population dynamics models, which show that dispersal limitation occurs only when the mean among-patch distance and the variation in establishment probability are high (Söderström & Herben, 1997). Expressed another way, models demonstrate that if a species is able to survive at all, it has the potential to colonize almost all available patches (*i.e.* it is habitat limited), whereas if the species is dispersal limited the mean/average distances between habitat patches increase (Söderström, 1998). Additional evidence from actual field studies also suggests that habitat availability may be more important than a plant's dispersal ability as a cause of *natural* rarity in bryophytes (Laaka-Lindberg, Hedderson & Longton, 2000).

Niche breadth is an important concept in bryology. It is based upon the premise that rare species utilise a relatively narrow range of resources, whilst more common species are able to use a broader range of resources and consequently occur in more places. An analysis of the bryophyte flora of Lancashire by Callaghan & Ashton (2008) demonstrated support for this concept and showed that two indicators of niche breadth, the range of habitats and substrates occupied by a species, are positively correlated with range-size. In other words, they showed that rare species occupy a significantly narrower range of habitat and substrate than more common species, both at the scale of the study area (Lancashire) and of the British Isles. Whilst this may be linked to dispersal ability of a species, habitat factors such as fragmentation and quality of patches are also important. Low occupation of apparently suitable sites has been observed by several workers and it seems that tolerances in bryophytes to habitat and substrates are related to initial establishment requirements (Söderström, 2005; Cleavitt, 2002; 2005) which are only poorly understood.

Returning briefly to the concept of life-history strategies, perennial species with large between-years fluctuations in colonization ability are affected less than short-lived species that need to recolonize frequently. Impaired reproduction may occur for a number of reasons, such as pollution and a species may be able to sit tight for as long as the habitat patch remains suitable. Shuttle species where within-patch dynamics is important are less affected than perennials or colonists and are most affected by a decrease in patch size. Metapopulation models predict that short-lived species with low dispersal ability will be most at risk from habitat fragmentation (Söderström, 1998); as noted earlier many of the Red Listed bryophytes in Britain have such a strategy.

Natural and human-induced rarity

This section has endeavoured to collate some of the inter-related factors that cause a bryophyte to be rare, including reproductive biology, life-history strategies and habitat dynamics. It seems that although habitat limitation would intuitively appear to be the cause of rarity in bryophytes, current evidence points to *dispersal limitation* as the cause of occurrence at few localities. Human pressure on the land has probably been responsible for this situation and it is likely to intensify as fragmentation and exploitation of habitats continue (Söderström & During, 2005). Callaghan & Ashton (2008) and Söderström & During (*op cit*) have put forward the view that most *naturally* rare bryophytes are habitat limited (narrow niche breadth) and able to survive as small but stable populations provided dispersal ability at least balances the local extinction rate. Such species have always been rare and probably always will be, and not all are necessarily threatened. For most declining bryophytes, the focus of this book, dispersal limitation would seem to be the reason for rarity. As the population size of a bryophyte decreases due to erosion of habitat patches – and fragmentation increases – there is a concomitant decrease in diaspore output, with the result that dispersal to available and ever more distant suitable habitat patches is compromised. It is this group of bryophytes that is threatened and represents *human-induced* rarity.

Conservation measures

Today ‘conservation’ is a well-worn term and is used in many contexts. Protection, guardianship, restoration, preservation and management are just a few of the words used to define it. This section aims to show how nature conservation is delivered in the wider sense and how *bryophyte* conservation impacts on the bryophyte flora of England. Conservation needs to operate at a number of complementary levels if it is to be effective. The two foremost measures to protect bryophytes in England are through habitat conservation (including habitat management, restoration or enhancement) and species conservation implemented through Action Plans or similar. Other valuable complementary approaches are *ex situ* conservation (such as off site in a botanic garden or similar) and translocation, for example moving or reintroducing a threatened bryophyte and thus reinforcing a diminished population. These actions are undertaken within a framework of processes and mechanisms and will be briefly considered in this section (for a discussion of bryophyte conservation activities in Europe see Porley *et al*. 2008).

Habitat conservation

England's bryophytes can only continue to exist if there is adequate quality habitat and good connectivity between patches, attributes shown to be important in the preceding discussion on rarity. Furthermore, bryophytes will be better equipped to deal with climate change impact and pollution events. Without exception, studies of the biology of rare bryophytes are united by one conclusion: that effort should be directed towards maintaining the largest possible areas of natural and semi-natural vegetation – in other words the habitat (Longton & Hedderson, 2000; Bisang & Hedenas, 2000; Cleavitt, 2005). This holds true for both common and rare species and for conserving genetic diversity.

Sites

Arguably, most of the high-quality habitat in England is contained within the Sites of Special Scientific Interest (SSSI) network. The Nature Conservancy Council (NCC), under the National Parks and Access to the Countryside Act 1949, began the selection and notification of SSSIs, latterly taken forward by English Nature (*EN*) under the Wildlife and Countryside Act 1981 (WCA 1981) with some notification being undertaken by the current statutory agency Natural England (*NE*). Bryophytes were invariably not part of the SSSI selection procedure in the early days of notification, but many were included *de facto.* There are some 4,114 SSSIs in England covering a total of 1,076,986 ha, or 8% of the total area of England (*NE*, 2008). The majority of SSSIs are small, with 40% less than 10 ha and 82% smaller than 100 ha. National Nature Reserves (NNR) – the jewels in the crown – of which there are 221 in England, cover an area of about 95,776 ha, although virtually all NNRs are also SSSIs. NNRs tend to be larger, with 56% being at least 100 ha or more in size. International site designations, such as those originating in the EU under the Habitats and Birds Directives that have been designated as Special Areas of Conservation (SACs) or Special Protection Areas (SPAs) respectively (collectively known as the Natura 2000 site network), plus the Ramsar wetland sites, cover some 884,623 ha of England, of which virtually all are also notified as SSSIs. Of the total semi-natural habitat in England, only about 48% lies within SSSIs. A large proportion of non-SSSI land is, however, contained within other designated areas such as National Parks (NP) and Areas of Outstanding Natural Beauty (AONB) and these alone cover 23% of England.

A preliminary investigation of the overlap of modelled and projected future climatically suitable regions for rare bryophytes within the current SSSI network was carried out by Anderson & Ohlemüller (2011). The proportion of hectare (10 × 10 km squares) records of rare bryophytes within 100 m of an SSSI was calculated and was shown to be low for Britain as a whole. It was particularly low for England, with half of the species having at least 62% of their hectare records within 100 m of an SSSI boundary [1]. The results also indicated that there are regions where rare bryophytes may be inadequately protected since there is not always an overlap between distribution of bryophyte records and SSSIs. For example, there is a high concentration of SSSIs in parts of N and W Yorkshire but few hectare records of rare bryophytes, whereas to the east of this area there are many bryophyte records but few SSSIs. There are areas of congruence; the New Forest in southern England is a good example. There could be many reasons to account for these observations and more field data with precise species coordinates is required. The results of the study therefore need to

[1] for Wales it was 75%, for Scotland 79%

be interpreted with caution but they do suggest that the current SSSI network is insufficient to safeguard English rare bryophytes from the effects of climate change.

It is well known that some species in other groups, such as orchids, are more or less confined to protected sites and this is certainly the case for many bryophytes as shown in the species profiles in this book. Monitoring work has shown that in groups characterized by very specific habitat requirements (such as birds, butterflies and bees) there has been a steep decline in individuals and populations (*NE*, 2008). Many bryophytes, as pointed out earlier, also have high habitat specificity and a narrow niche breadth and are thus likely to be under similar pressures.

Species conservation

Ultimately, nature conservation comes down to species – the plants and animals that share our world. It is essential to know which species are threatened and, provided that the reasons why are understood, conservation measures can be taken. For the majority of bryophytes, habitat conservation is inseparable from species conservation and may be the only measure needed. But for some bryophytes, actions which are specifically tailored to the needs of an individual population may also be necessary to address the decline.

Species conservation operates through several processes and mechanisms. In the early days of statutory nature conservation in England, bryophytes were given scant attention and protection was largely incidental to that of either the habitat or other species groups. The seminal *A Nature Conservation Review* (Ratcliffe, 1977) may well have kindled the first stirrings of organised bryophyte conservation in England. This two-volume work recognized the importance of mosses and liverworts and included bryophyte lists in accounts of major biotopes and sites. Although the statutory conservation community was slow to take up the cause of bryophytes, the British Bryological Society (BBS) was acutely aware of the threats many bryophytes were facing and played an important role in persuading others to take bryophyte conservation seriously.

SSSIs were not selected for their bryophyte interest until 1992, when selection guidelines were published (Hodgetts, 1992) in which species were ranked and scored according to a suite of established criteria. Hereafter a site could be designated on bryophyte interest alone. Where such a species or habitat is chosen, it is termed a notified feature, or a species could be part of the reason for designation alongside other species groups or the habitat. These guidelines have not kept pace with our knowledge of bryophyte distributions nor their current status based on IUCN criteria and are in urgent need of updating. The data are not available giving the number of English SSSIs with *bryophytes* specifically as a notified feature, but the number of SSSIs in which non-vascular plants (bryophytes, lichens, algae etc.) are included as a notified feature is 184 (*NE*, 2008). An estimate would be that very few sites, probably six at the most (and all in Cornwall), are notified for their bryophyte interest alone. Every SSSI is assessed on a six-year cycle using the Site Condition Monitoring framework developed by the Joint Nature Conservation Committee (JNCC) in association with the statutory agencies. Whilst a Public Service Agreement (PSA) target to achieve 95% of SSSI area in favourable or recovering condition by 2010 was achieved, it does not tell us how bryophytes are faring on those SSSIs. It has been acknowledged that better surveillance of bryophytes is needed in England's natural environment (*NE*, 2008).

UK Biodiversity Action Plans (BAP)

What was to be perhaps the most significant advance in bryophyte conservation came when the UK government signed up to the first global agreement, the Convention on Biological Diversity (CBD), at the 1992 Rio Earth Summit. Two years later the UK Biodiversity Action Plan (UK BAP) was published, the UK government's response to the CBD, containing six moss and five liverwort Action Plans. By 1999, there was a total of 35 moss Action Plans and 11 liverwort Action Plans. It is these plans that have so effectively focused action on English bryophytes and their value is evident in many of the species profiles in this book. Following a two-year review of the UK BAP programme starting in 2005, a new bryophyte list based largely on the previous Red List (Church *et al*., 2001) was published in 2007, and this effectively more than doubled the number of bryophytes on the UK BAP (111 in total, 77 in England). Regrettably, due to resource constraints, many species Action Plans have not yet been written (although JNCC has produced species statements) and there has been variable progress on those that have been published.

The UK BAP review was used as the basis for *NE* to draw up the list of species and habitats of principal importance in England under Section 41 (S41) of the Natural Environment and Rural Communities (NERC) Act 2006. The 77 bryophytes herein are considered to be of principal importance for the purpose of conserving biodiversity in England and, in essence, the Secretary of State (and organisations with the corresponding Public Duty) must take such steps as appear reasonably practicable to further the conservation of the species (and habitats) on the list and promote others taking such steps. Since the S41 bryophyte list was drawn up prior to the publication of the revised Red List of British bryophytes (Hodgetts, 2011) there is currently a mis-match between the two lists. There are 18 species on S41 that are not on the Red List; most of these are currently classified as Near Threatened and include species such as *Dendrocryphaea lamyana*, *Habrodon perpusillus*, *Leptodontium gemmascens* and *Petalophyllum ralfsii*. On the other hand, some 27 Red List species are not on S41, including *Anomdodon attenuatus*, *Didymodon cordatus*, *Nardia insecta* and *Tomentypnum nitens*. Of the 87 British Red List species in England, 61 are on the UK BAP list.

Legislation

Special protection is conferred on 37 British bryophytes listed on Schedule 8 under Section 13 of the WCA 1981. The list includes six liverworts and 17 mosses that occur in England, one species (*Bartramia stricta* (see *Appendix 1*)) that is extinct in England, and two species (*Bryum mamillatum* and *B. neodamense*) that have since been synonymized with other species. The benefit of listing on Schedule 8 has long been debated since there was little confidence that the regulations would be enforced, but few would deny that it fulfilled an important role in raising the profile of rare bryophytes and facilitated the protection of the sites on which they occur. The 1992 selection guidelines for lower plants states that a site should be considered for SSSI notification if it supports a viable population of a Schedule 8 plant, and indeed was often used in the justification for notifying a site on its bryophyte interest alone. The bryophytes listed on Schedule 8 have been subsumed, unrevised, into new legislation including the Countryside and Rights of Way (CROW) Act 2000 and. most recently. in Part 2 of the Natural Environment and Rural Communities (NERC) Act 2006.

Regardless of the perceived weaknesses of Schedule 8, there seems more willingness to take legal action concerning the 77 English UK BAP priority bryophytes. In 2003, the first occupier prosecution under the CROW Act 2000 was brought by *EN* for significant damage to rare bryophytes. The incident concerned the West Cornwall Bryophytes SSSI in which the occupier