

Oikos Editorial Office

Trends in Bryophyte Population Dynamics

Author(s): Heinjo J. During

Source: *Lindbergia*, Vol. 31, No. 1/2, The State of Bryophyte Ecology 2005 (2006), pp. 6-15

Published by: [Oikos Editorial Office](#)

Stable URL: <http://www.jstor.org/stable/20150202>

Accessed: 17/08/2011 15:56

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Oikos Editorial Office is collaborating with JSTOR to digitize, preserve and extend access to *Lindbergia*.

<http://www.jstor.org>

Trends in bryophyte population dynamics

Heinjo J. During

During, H. J. 2006. Trends in bryophyte population dynamics. – Lindbergia 31: 55–64.

Rapid advances in the field of bryophyte population dynamics include the development of non-destructive techniques to mark and monitor individual shoots, which allowed the construction and sophisticated use of matrix models and the analysis of the consequences of fine-scale dynamics and sexual reproduction for shoot survival and growth. Dissection of turfs of desert bryophytes yielded additional evidence, as well as more detailed knowledge on phenological patterns and year-to-year variation in investments in reproduction. Studies of population dynamics at larger spatial (metapopulations) and temporal (diaspore banks) scales included experimental and modelling work on spore dispersal and on conditions favourable to spore germination and establishment, as well as extension of current metapopulation models to explicitly incorporate the dynamics of the habitable patches themselves. Together with the rapid advance of molecular techniques allowing genet recognition and the analysis of parent-offspring relations, these new developments now open the way to study the dynamics of populations of genets, which is a necessary prerequisite for a more in-depth analysis of rates and directions of processes of natural selection and evolutionary change.

H.J. During (h.j.during@bio.uu.nl), Dept. of Plant Ecology, Utrecht Univ., F.A.F.C. Went Building, P.O. Box 80084, NL-3508 TB Utrecht, the Netherlands).

Bryophytes have complex life histories, with a prominent role for clonal propagation. Add their small spore size, the often tremendous numbers of spores produced, of which only a tiny fraction may ever germinate and establish, and their large potential for long-range dispersal (at least compared to phanerogams), and it may be clear that a quantitative study of the processes underlying bryophyte population dynamics, and in fact quantification of the dynamics itself, is not an easy job. Major problems include 1) recognition of genets; 2) causes of shoot mortality; and 3) factors and processes affecting successful establishment after germination (During and Van Tooren 1987).

Yet, in the last decades bryologists have been very successful in their attempts to describe the dynamics

of shoots in colonies, of turfs, cushions and the like in a community context, and of populations in a fragmented landscape, and to unravel the mechanisms involved and environmental ‘filters’ affecting them. Taken together, these studies show that the field has strongly diversified, and now is ‘viewed through multifocal lenses’, with increasing attention for processes at different spatial and temporal scales and their interactions.

Shoot dynamics

Early studies of bryophyte dynamics employed repeated micro-charting of shoot populations (Egunyomi 1978, During and ter Horst 1985), but did not try to construct actual life tables of the populations. The accuracy of this technique strongly depended on the grain of the population sampled, but even for large species reliable estimates of mortality and especially

of shoot natality proved to be very hard to obtain. It was obvious, however, that even within species shoot mortality risk, for example, strongly depended on shoot size. An extension of this technique, based on estimates of species abundances in small cells of a grid, provided interesting data on small-scale dynamics and the pattern of these dynamics (spatial autocorrelation of growth and mortality, During and Lloret 1996; competitive exclusion of the short-lived species *Tayloria tenuis*, Lloret 1991), but did not allow a thorough analysis at shoot level either.

Using a combination of photographic and stratigraphic techniques to monitor shoot populations of *Polytrichum alpestre* in the Antarctic, Collins (1976) was able to estimate rates of natality and mortality, and describe shoot density/biomass relations.

In their study of the shoot dynamics of *Polytrichum piliferum*, Hobbs and Pritchard (1987) similarly used sequential photographs to obtain 'dynamic life table' data (Begon et al. 2005), and produced 'static life table' data by reconstructing the history of excavated clone parts using innate markers based on leaf size variation. Long-term monitoring proved to be problematic, however, as it led to increasing shoot mortality. Vitt (1991) used photographic techniques to monitor growth of *Racomitrium microcarpon*, and was able to get accurate data on shoot growth, but demographic analysis was restricted to an estimate of the age distribution of the *Racomitrium* patches present on the rock. Apparently, the spatial resolution and repeatability of these techniques was insufficient to accurately monitor the fate of large numbers of individual shoots, and thus to provide data on the rates of shoot mortality and persistence and the establishment of new shoots.

Use of small, coloured plastic rings (Rydgren and Økland 2002a) allowed Økland and co-workers (Økland 1995, 2000, Økland and Økland 1996, Rydgren and Økland 2001, 2002b, 2002c, 2003) for the first time to monitor all individuals of *Hylocomium splendens* in permanent plots, and thus obtain estimates of the vital rates of such populations. This approach allowed the authors to construct dynamic life tables and matrix projection models for these populations. Based on the dominant eigenvalues of the matrices and the elasticities of the individual matrix entries the authors concluded, that population maintenance heavily relied on survival and continuation of mature shoots, rather than recruitment of additional growing points (Økland 1995, 1997). Further analyses on the fates of shoots of different size classes in conjunction with their vertical position in the moss canopy and the local shoot density showed, that shoot growth was positively correlated with density, while size-correlated shoot mortality was not related to density and recruitment from new growing points de-

clined with increasing density (Økland and Økland 1996, Økland 2000). The largest shoots had the highest probability to produce sporophytes, while sporophyte production itself negatively affected next-year shoot growth and branching (Rydgren and Økland 2001).

The shoot-marking technique used in these studies has been used for other large pleurocarps, but it may be less easily applicable to small liverworts and acrocarpous mosses growing in dense turfs (Weibull 2000, Rydgren and Økland 2002a). However, as shown by the detailed study of *Crossidium crassinerve* by Stark and Delgadillo (2003), in some cases it is possible to make use of innate growth markers to identify annual segments and so provide data to construct a static life table. Whether this will allow estimates of vital rates such as provided by the actual monitoring of shoots through time remains to be seen, but at least it has already drastically changed our intuitive view of the potential life span of these plants – the shoots of this *Crossidium*, usually considered as annual or paucennial, may actually reach ages of 50–75 years!

Genet dynamics

Although the analysis of shoot dynamics is an important tool in understanding, e.g. the control of shoot growth and the mechanisms behind competitive exclusion and the consequent microsuccession, from an evolutionary viewpoint population dynamics should deal with genets. Data on this level are essential for estimates of generation times, rates of selection processes, etc. For this purpose, molecular methods are essential. For species with plants that are large enough to allow extraction from individual shoots, allozymes already open possibilities in this direction, as was shown, e.g. in the exemplary study of Cronberg (2002) on the population dynamics of *Hylocomium splendens* on ten islands of various ages in a Baltic land uplift area. Cronberg convincingly demonstrated, that there was a slow but steady increase of the number of genotypes per island with age, with an average rate of 15 clones per 200 years, showing that the species should behave in the same way as RSR (repeated seedling recruitment) species among phanerogams do (Eriksson 1993). The genetic analyses did not reveal any isolation by distance among the populations, which suggested that recruitment primarily occurred by spores originating from mainland populations at some distance from the islands rather than by spores produced locally. Local distribution of genets gradually expanded by asexual propagation with increasing colony age, leading to spatial extension of genets over distances of up to 6.4 m. Simultaneously, the

degree of mixing of genets within colonies also increased with age, and on the oldest islands (over 300 years old) sporophytes started to be produced, indicating close intermingling of male and female genets and successful gamete production of both sexes.

Qualitatively similar results have been found for *Plagiomnium affine* in planted Swedish forests of varying age, again using allozymes (Cronberg et al. 2003): number of genotypes per population, degree of clone mixing and frequency of sporophyte production gradually increased with forest age. In this species, an additional factor leading to more intermingling of genotypes and higher frequency of sporophytes appeared to be frequent disturbance by badgers, presumably by increasing clone fragmentation and local dispersal of these fragments, and perhaps increased growth rates of the plants as a consequence of reduced competition and enhanced nutrient supply due to the disturbance.

With the current rapidly increasing availability and ease of PCR-based techniques, studies of genet dynamics and associated aspects of bryophyte population ecology (e.g. phylogeography, Chiang and Schaal 1999) may be expected to boom (Goffinet 2003). As an example, the determination of paternity of sporophytes of *Polytrichum formosum* provided accurate estimates of the distance of male gamete dispersal in this splash-cup-forming species (Van der Velde et al. 2001).

Matrix models for complex life cycles

Matrix models based on shoot dynamics can be quite helpful in analyzing consequences of competition and other density-dependent processes. But more evolutionarily oriented investigations such as invasibility of populations by rare genotypes, consequences of genetic drift or the importance of outcrossing events in monoecious species need an analysis of data at the genet level. This concerns not only the rate of establishment of new genotypes in a population, but also the probability of genet mortality and genet growth rates, well-known problems in clonal-plant population ecology (Eriksson 1994). In principle, matrix models involving only numbers of genets in different size classes would already be helpful. But by leaving out any explicit treatment of the physical interactions between the ramets and the consequences of genetic variation in ramet morphology, anatomy and/or physiology, such models are not very suitable to analyze the mechanistic consequences of the introduction of new genotypes or other aspects of genetic variation. To some extent inclusion of such aspects is possible in a range of models, from very simple to fairly complex, which have recently been proposed for species

with biphasic life cycles (Thornber and Gaines 2004), i.e. for species with alternating, free-living haploid and diploid phases. Predictions of the models were tested using data of three isomorphic algae, *Mazzaella* spp.

All models shared the following assumptions: the populations are characterized by an obligate alternation of independent, free-living, haploid and diploid phases; demographic rates do not vary in time; male gametes are non-limiting; and the sex ratio of the haploid spores is 50:50. If vital rates (mortality, fecundity, etcetera) would be the same for haploids and diploids, all models predict a stable distribution with a ratio of 2 : 1 (about 60% haploids, 40% diploids). In some *Mazzaella* species, however, both mortality rates and fecundity of diploids were higher than those of haploids, both of which contributed to a stronger dominance of haploids in the populations – increased diploid mortality leads to a lower frequency of diploids, and increased diploid fecundity leads to the production of more haploids. Furthermore, the models contributed to the understanding of the consequences of differences in dispersal of the gametes, c.q. spores, produced by both stages (and consequently, of lifting the assumption that male gametes are non-limiting and all egg cells on the female thalli are fertilized), and of density dependence of the vital rates.

Although the model is not unrestrictedly applicable to bryophytes, albeit only because the diploid stage in bryophytes is not independent and free-living, it may be worthwhile to think of bryophyte population dynamics along these lines, especially because the haploid and diploid phases do strongly differ in their vital rates. Thus, haploid genets are usually polycarpic and have a flexible life span due to extensive asexual propagation, while diploid genets (sporophytes) are always monocarpic ('big-bang' reproduction) and are characterized by a relatively fixed life span. From this perspective it is obvious, why sporophyte abortion is so important (Stark et al. 2000, Stark 2001, 2002). Yet, young sporophytes seem to be less well defended against herbivory than gametophytes (Davidson et al. 1990), which according to these models should lead to an increased haploid fraction in the population. The few species tested so far seem to differ in palatability of gametophytes and young sporophytes; it would be worthwhile to have a more systematic study of the palatability of species with different life strategies. Whether sporophytes and gametophytes also differ in their sensitivity to microfungi or other parasites is not known either.

By far the most important practical problem, however, concerns the mortality between census dates, especially of offspring. Matrix models characteristically describe transitions between life-history stages

over discrete (say, one-year) time steps, and consequently, either the fertility rates (numbers of gametes, c.q. spores, produced) or the survival rates of ‘newborn’ over the first time step should include their success rate: either successful fertilisation of an egg, or successful dispersal and establishment (c.q. survival in the diaspore bank) of spores. These probabilities are extremely small and probably very difficult to quantify – e.g. in the very detailed analysis of the population dynamics of *Anastrophylum hellerianum*, success rate of spore germination and establishment in the field is the only obvious ‘missing value’ (Pohjamo and Laaka-Lindberg 2003, 2004; Table 1). Yet, there have been some encouraging developments in this area, involving, i.a.

- rates and mechanisms of dispersal of asexual propagules of hepatics (Laaka-Lindberg et al. 2003, Pohjamo et al. 2006) and mosses (Kimmerer and Young 1995).
- seasonal and long-term dynamics in diaspore banks (During 2001, Hock et al. 2004).
- mortality of (un-)germinated spores in the field (Miles and Longton 1990).
- ecological conditions, position and extent of patches suitable for successful germination and establishment (Sundberg and Rydin 2002, Wiklund 2003, Wiklund and Rydin 2004).
- reproductive effort and costs of reproduction for sporophyte-bearing female shoots (Ehrlén et al. 2000, Bisang and Ehrlén 2002, Rydgren and Økland 2002b, 2003) and for female and male gametangia production (Stark et al. 2000, Crowley et al. 2005).
- mate limitation of reproductive success in dioecious species (Bisang et al. 2004).

Actual dispersal patterns have been studied primarily over fairly short distances within communities (Miles and Longton 1992, Jonsson and Söderström 1988, Pohjamo et al. 2006), but models of dispersal processes such as that of Sundberg (2005) gradually are able to account for the notorious ‘fat-tail’ problem – the fact that dispersal over really long distances is usually underestimated by traditional spore deposition curves (Bullock and Clarke 2000). Yet, it is exactly this long-distance dispersal that is responsible for rates of change in distribution area in times of rapid environmental change such as we witness now (Hassel et al. 2005), for expansion rates of invasive exotics (Herben et al. 1991), and for gene flow between widely separated populations in a metapopulation (Söderström and Herben 1997).

Table 1. Demographic rates of the epixylic liverwort *Anastrophylum hellerianum* (after Pohjamo and Laaka-Lindberg 2003, 2004).

gemmae per shoot	1200
transition gemma → sterile shoot	0.0015
idem → fertile shoot	0.0002
transition sterile → gemmiferous shoot	0.577
transition sterile → fertile shoot	1.122
spores per capsule	12000
colonies with sporophytes: 3/25	0.12
females with sporophytes in such colonies	0.076
fertility per female: $0.12 \times 0.076 \times 12000$	109.44
spore germinability under laboratory conditions	0.4
successful germination and establishment in the field?	?

Scaling up in space: a metapopulation approach

Some bryophytes seem to be very long-lived, with the tufa-forming *Hymenostylium recurvirostre* (2800 years, Reichard 1860) as perhaps the most striking documented example. Obviously, populations of such species tend to be persistent as well. In most species, however, local populations are fairly short-lived, and species persistence depends on the balance between colonisation rate of new or empty habitat patches and local extinction. For such species, Levins (1969) coined the term metapopulation dynamics.

The rate of colonization of new patches is determined by the distance between patches, the numbers of propagules produced, the per-diaspore establishment probability (Herben and Söderström 1992), and dispersal rates as affected by diaspore size and dispersal agent – e.g. directed spore dispersal by animals (Splachnaceae: Koponen 1990; *Schistostega pennata*: Ignatov and Ignatova 2001) is much more effective than wind dispersal.

Local extinction may be due to biotic (e.g. competitive exclusion) or abiotic factors (e.g. catastrophic disturbances), but it may also reflect the limited life span of the patch itself. While boulders in a forest may provide opportunities for colonisation and establishment for ages (Kimmerer and Driscoll 2001, Weibull and Rydin 2005), trunks and branches of living trees (Hietz 1997, Snäll et al. 2003) and rotten logs of fallen trees (Kruys et al. 2002) will usually last a lot shorter, as will the dung patches in mires on which *Splachnum* species and relatives specialize (Marino 1997). Even the dynamics of epiphylls on tree leaves may be described using metapopulations models (Zartman 2003).

Metapopulation ecologists have long recognized the importance of patch destruction for the survival probabilities of the metapopulation (Hanski 1998), but

the explicit consideration of the dynamics of the patch structure of a landscape is fairly new. One of the first attempts to formalize this was the matrix model of patch dynamics of rotten logs of Kruys et al. (2002). For rich-bark epiphytes in boreal forests, the dynamics of the substrate operate even at two scales in time and space: individual trees of the best phorophyte, *Populus tremula*, have a limited life span, but they also occur in widely separated patches in the forest which eventually tend to be overgrown by conifers (Hedenäs et al. 2003). Models explicitly taking the patch dynamics at these two scales as recently proposed by Snäll et al. (2005a, 2005b) look very promising, but also quite demanding in terms of mathematics. Still, it seems to be possible in this way to estimate with some degree of reliability, to what extent the patch structure and dynamics in this system allow persistence of the different epiphytes on these trees, with their different propagule types (spores, gemmae, stem fragments) and associated dispersal capacities.

The metapopulation approach plays an increasingly important role in nature conservation – fragmentation (Pharo et al. 2004), isolation, edge effects, invasive species, and many other conservation problems ultimately refer to a metapopulation perspective. In that respect, the incorporation of these different scales in metapopulation models is very promising, and eventually should allow us to assess, whether species are seriously threatened or just showing ‘normal’ dynamics (During 2000, Söderström and During 2005).

Also from a more theoretical viewpoint the metapopulation approach can provide valuable insights, however. An interesting example is provided by a study of the dynamics of the dioecious hepatic *Marchantia inflexa* by D. N. McLetchie and collaborators. Male and female thalli differed slightly in their rates of thallus growth, production of new thallus apices and gemmae, with females being more competitive and producing more thallus apices and less gemmae, while local (i.e. within-boulder) recolonisation of empty patches almost exclusively took place via expansion of existing thalli or establishment of asexual diaspores (McLetchie and Puterbaugh 2000). In the habitat under study, a river valley on Trinidad, the species occupied boulders along the river. A population model suggested, that coexistence of males and females on individual boulders would not last indefinitely, and that females would outcompete males on all but the most frequently disturbed boulders (McLetchie et al. 2002). Occasionally, however, boulders would be completely cleared of vegetation by thunderstorms or other local disasters, and then recolonisation was mainly by spores – and since the sex ratio of spores of this species is 50:50, as in most dioecious bryophytes, and there was no obvious dif-

ference in establishment rate between the sexes, new populations thus would start with equal numbers of males and females! So, a metapopulation perspective contributed to a better understanding of the mechanisms stabilising the sex ratio of the population and thus, maintaining a high frequency of sexual reproduction (see also Crowley et al. 2005).

Population dynamics in a community context: consequences of positive density dependence

The theoretical framework behind population dynamics strongly relies on feed back mechanisms involving negative density dependence (Yodzis 1989). Positive density dependence (e.g. better growth at higher densities) has occasionally been recognized as an option (Goldberg and Werner 1983), and increasingly found to actually occur in nature, but only recently ecologists realized themselves how pervasive the consequences of this phenomenon are for much of ecological theory, including population dynamics (Bruno et al. 2003).

In bryophytes, negative relations between shoot size and density have been found repeatedly (Clymo 1970, Collins 1976, Pohjamo and Laaka-Lindberg 2004) and were usually interpreted as the logical consequence of an increase of competition for light at higher densities (Clymo and Hayward 1982). Økland and Økland (1996), however, found a positive relation between shoot size and density in *Hylocomium splendens*. Bates (1988) was one of the first to experimentally demonstrate positive density-dependence in *Rhytidiadelphus triquetrus*, and to show the underlying mechanism: although a higher density leads to stronger competition for light, the positive effect on the length of periods during which the water content of the shoots is adequate for a positive carbon balance apparently dominated the effect of density on growth. Similar results were obtained by Van der Hoeven and During (1997). In an experiment with *Dicranum majus* and *Rhytidiadelphus loreus* Hanslin et al. (2001) showed, that the relation of the RGR (relative growth rate) and shoot density was unimodal, and that the density at which growth was highest depended on air humidity. Using a combination of a phenomenological model and a multifactorial experiment in which the same two species plus *Plagiochila asplenioides* and *Ptilium crista-castrensis* were grown at different densities, light intensities and air humidities, Pedersen et al. (2001) confirmed that an increase in shoot density has both positive and negative effects on shoot growth (related to shoot moisture content and light penetration into the canopy, respectively), although their results suggest, that under the boreal forest floor conditions at which these species occur in the field, the negative effects of com-

petition for light would predominate. The rapid recovery of *Hylocomium splendens* after fine-scale disturbances observed by Rydgren et al. (2001) would also point in this direction.

An important element in the explanation of the underlying mechanism is the effect of shoot density on the wind speed profile in the bryophyte canopy. Simple downscaling of existing models for tree canopies did not seem to work well (Proctor 1980), but using an ingenious technique Rice et al. (2001) were able to show how the roughness length of the bryophyte canopy could be quantified and put in relation to the wind profile and the associated loss of water vapour. Later Rice et al. (2005) presented a simpler method using a simple laser scanner for the same purpose.

The positive relation between diversity and productivity predicted by this model also plays an important role, but from a different perspective, in the work of Mulder et al. (2001) and Rixen and Mulder (2005), who focus on the role of diversity for community performance, i.e. productivity. Mulder et al. (2001) found, in artificial bryophyte stands kept for a year at low light and continuously high air humidity, that diversity enhanced productivity after a five-days drought treatment, but did not so under “control” conditions without drought. Moreover, the species which were least resistant to drought in monoculture increased most strongly in biomass at high diversity. Rixen and Mulder (2005) obtained similar results in artificial stands at a range of diversities (1–11 species) in an Alaskan tundra and in a greenhouse. Working at two densities, which had been created by changing concentration of moss slurry at sowing, they analyzed the effects of short vs long drought treatments. Also in this experiment diversity had a positive effect on biomass production, especially at low densities. A path analysis suggested, that this effect might be attributed to improved humidity conditions at high diversity.

These results are certainly interesting, but many questions remain, e.g. – even if there is a direct effect of diversity on productivity, we still have no clue as to what mechanism maintains the high diversity. It would also be interesting to know, whether the results also apply to bryophytes in a vascular plant matrix. Preliminary observations of pleurocarps completely filling the space inside dwarf shrubs in Dutch dune heath do suggest, that under some conditions wind braking by phanerogams may be beneficial to bryophyte growth. Competition between bryophytes and vascular plants may be severe as well.

Future perspectives

First of all, there is a clear need for further quantification of ‘basic’ population processes such as dispersal, conditions for successful establishment and causes of mortality. Thus, we still have insufficient ideas about what constitutes possible (‘safe’) sites independently of the plant growing there itself – an essential element of the metapopulation concept. In this respect, we should not forget a simple but important problem: how to extend the techniques found suitable in the few ‘model species’ used so far to a wider range of species with different morphologies. For example, most current metapopulation models refer to epiphytes or corticolous species, i.e. species without a long-lived diaspore bank. For many soil-inhabiting species, however the importance of such a diaspore bank is obvious, but there has hardly been any attempt to incorporate this aspect into metapopulation models.

The rapid advances in the current molecular methods will have a tremendous impact on the whole field of population dynamics. First of all, monitoring of genets and the analysis of genet dynamics will become much less complicated and expensive. Consequently, e.g. comparative demographic studies on groups of species with contrasting growth forms, life forms or life histories will provide a firmer basis for life strategy classifications.

Another field of rapid advances is parent-offspring analysis. It is now possible to identify the father of a sporophyte (Van der Velde et al. 2001) and to analyze kinship relations over a range of spatial scales (Snäll et al. 2004). The results of such studies have already proven to be essential in tackling phylogeography, gene-flow, long- and short-range dispersal problems, and will rapidly become more prominent in the future, and help to address questions such as: how important is genetic variation for long-term persistence of (meta-)populations? If we also would have a better understanding of the processes causing mortality, we might get some information concerning the scale of synchronous mortality events, and we could tackle questions such as: does risk spreading as a result of clonal propagation lead to increased genotype evenness and genetic diversity of a population with site age? This pattern has been found in *Circaea lute-tiana*; simple random-walk model studies suggest, that this is only possible if ramet mortality somehow is affected by genet size, e.g. due to increased pathogen load on locally abundant genets or spatially clustered ramets (Verburg et al. 2000), but there is not much experimental evidence of such effects of genet size. Yet, Cronberg’s (2002) data on *Hylocomium splendens* do suggest that this may also apply to bryophytes.

In spite of the current emphasis on 'neutral theories' and 'null models', ecological theory still relies heavily on interspecific interactions (herbivory, predation, pathogens) and density-dependent processes such as competition and, increasingly, facilitation. This means that the performance of an individual ('fitness', often fertility or growth) should not be evaluated in absolute terms, but relative to the performers of other individuals with which the 'target' individual interacts – other 'players in the game' (Maynard Smith and Price 1973). Often, the analysis will show a 'tragedy of the commons' (Hardin 1968) – the evolutionarily stable strategy (ESS) often implies a much lower performance than that suggested by simple optimisation models. While this principle was soon embraced by many animal and theoretical ecologists (Maynard Smith 1982), it has only recently gained support in plant ecology, although Riechert and Hammerstein (1983) already showed the relevance of this approach to the analysis of root allocation strategies. Recent model studies and experiments showed, that plants competing with neighbouring individuals invest much more in leaf area (in the case of aboveground competition, Schieving and Poorter 1999) or roots (with belowground competition; Gersani et al. 2001) and, consequently, much less in seeds, than they do when growing in isolation. Such a game-theoretical framework has not yet been widely applied to bryophytes (but see Crowley and McLetchie 2002, Crowley et al. 2005), but this may change soon. The remarkable plasticity in morphological and physiological characteristics of bryophytes in response to environmental differences, in combination with genetic variation in the same characteristics as well as in their plasticity (Cronberg 2004), provide great challenges, but also ample opportunities. It will be fascinating to see, which consequences extensive clonality and positive density dependence will have in the context of game theory, and then bryophytes may well be discovered to be very suitable model organisms.

Finally, there is increasing evidence that bryophytes interact in many ways with other organisms in ecological networks. Although their palatability for most animals seems to be low (Davidson et al. 1990), bryophytes are eaten by a range of animals (Gerson 1982). Moreover, bryophytes strongly affect the physical (temperature, humidity) environment of many small animals. Where they form a large part of the plant biomass, bryophytes also have much larger-scale effects by considerably changing albedo and thermal isolation characteristics of the ground surface (Berlinger et al. 2001). Also the chemical environment of associated plants and animals may be bryophyte-dependent (think of the role of *Sphagnum* in bogs). Carnivorous bryophytes, however, seem to be rare

(Barthlott et al. 2000). Bryophyte-fungus interactions are multifarious (Read et al. 2000), presumably even including mycorrhizal connections to neighbouring vascular plants (Bidartondo et al. 2003). Furthermore, bryophytes are engaged in diffuse interactions with algae, vascular plants and other bryophytes (During and van Tooren 1990). Better insight in bryophyte population dynamics will ultimately be required for a quantitative understanding of the roles that bryophytes play in ecosystems.

References

- Barthlott, W., Fischer, E., Frahm, J. P. et al. 2000. First experimental evidence for zoophagy in the hepatic *Colura*. – *Plant Biol.* 2: 93–97.
- Bates, J. W. 1988. The effect of shoot spacing on the growth and branch development of the moss *Rhytidiadelphus triquetrus*. – *New Phytol.* 109: 499–504.
- Begon, M., Townsend, C. R. and Harper, J. L. 2005. *Ecology – from individuals to ecosystems* (4th ed.). – Blackwell.
- Berlinger, J., Lynch, A. H., Chapin III, F. S. et al. 2001. The representation of arctic soils in the land surface model: the importance of mosses. – *J. Climate* 14: 3324–3335.
- Bidartondo, M. I., Bruns, T. D., Weiss, M. et al. 2003. Specializes cheating of the ectomycorrhizal symbiosis by an epiparasitic liverwort. – *Proc. R. Soc. Lond. B* 270: 835–842.
- Bisang, I. and Ehrlén, J. 2002. Reproductive effort and cost of sexual reproduction in female *Dicranum polysetum*. – *Bryologist* 105: 384–397.
- Bisang, I., Ehrlén, J. and Hedenäs, L. 2004. Mate limited reproductive success in two dioicous mosses. – *Oikos* 104: 291–298.
- Bruno, J. F., Stachowicz, J. J. and Bertness, M. D. 2003. Inclusion of facilitation into ecological theory. – *Trends Ecol. Evol.* 18: 119–125.
- Bullock, J. M. and Clarke, R. T. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. – *Oecologia* 124: 506–521.
- Chiang, T. Y. and Schaal, B. A. 1999. Phylogeography of North American populations of the moss species *Hylocomium splendens* based on nucleotide sequences from the internal transcribed spacer 2 of nuclear ribosomal DNA. – *Mol. Ecol.* 8: 1037–1042.
- Clymo, R. S. 1970. The growth of *Sphagnum*: methods of measurement. – *J. Ecol.* 58: 13–49.
- Clymo, R. S. and Hayward, P. M. 1982. The ecology of *Sphagnum*. – In: Smith, A. J. E. (ed.), *Bryophyte ecology*. Chapman & Hall, pp. 229–289.
- Collins, N. J. 1976. Growth and population dynamics of the moss *Polytrichum alpestre* in the maritime Antarctic. – *Oikos* 27: 389–401.
- Cronberg, N. 2002. Colonization dynamics of the clonal moss *Hylocomium splendens* on islands in a Baltic uplift area: reproduction, genet distribution and genetic variation. – *J. Ecol.* 90: 925–935.
- Cronberg, N. 2004. Genetic differentiation between populations of the moss *Hylocomium splendens* from low

- versus high elevation in the Scandinavian mountain range. – *Lindbergia* 29: 64–72.
- Cronberg, N., Andersson, K., Wyatt, R. et al. 2003. Clonal distribution, fertility and sex ratio of the moss *Plagiomnium affine* (Bland.) T.Kop. in forests of contrasting age. – *J. Bryol.* 25: 155–162.
- Crowley, P. H. and McLetchie, D. N. 2002. Tradeoffs and spatial life-history strategies in classical metapopulations. – *Am. Nat.* 159: 190–208.
- Crowley, P. H., Stieha, C. R. and McLetchie, D. N. 2005. Overgrowth competition, fragmentation and sex-ratio dynamics: a spatially explicit, sub-individual-based model. – *J. Theor. Biol.* 233: 25–42.
- Davidson, A. J., Harborne, J. B. and Longton, R. E. 1990. The acceptability of mosses as food for generalist herbivores, slugs in the Arionidae. – *Bot. J. Linn. Soc.* 104: 99–113.
- During, H. J. 2000. Life history characteristics of threatened bryophytes. – *Z. Ökol. Naturschutz* 9: 19–26.
- During, H. J. 2001. Diaspore banks. – *Bryologist* 104: 92–97.
- During, H. J. and ter Horst, B. 1985. Life span, mortality and establishment of bryophytes in two contrasting habitats. – *Abst. Bot.* 9, Suppl. 2: 145–158.
- During, H. J. and van Tooren, B. F. 1987. Recent developments in bryophyte population ecology. – *Trends Ecol. Evol.* 2: 89–93.
- During, H. J. and van Tooren, B. F. 1990. Bryophyte interactions with other plants. – *Bot. J. Linn. Soc.* 104: 79–98.
- During, H. J. and Lloret, F. 1996. Permanent grid studies in bryophyte communities I. Pattern and dynamics of individual species. – *J. Hattori Bot. Lab.* 79: 1–41.
- Egunyomi, A. 1978. Autecology of *Octoblepharum albidum* Hedw. in western Nigeria I. Growth and competition. – *Nova Hedw.* 29: 665–674.
- Ehrlén, J., Bisang, I. and Hedenäs, L. 2000. Costs of sporophyte production in the moss, *Dicranum polysetum*. – *Plant Ecol.* 149: 207–217.
- Eriksson, O. 1993. Dynamics of genets in clonal plants. – *Trends Ecol. Evol.* 8: 313–316.
- Eriksson, O. 1994. Stochastic population dynamics of clonal plants: numerical experiments with ramet and genet models. – *Ecol. Res.* 9: 257–268.
- Gersani, M., Brown J. S., O'Brien E. E. et al. 2001. Tragedy of the commons as a result of root competition. – *J. Ecol.* 89: 660–669.
- Gerson, U. 1982. Bryophytes and invertebrates. – In: Smith, A. J. E. (ed.), *Bryophyte ecology*. Chapman & Hall, pp. 291–332.
- Goffinet, B. 2003. Bibliography of systematic and population genetic studies of bryophytes based on DNA data. II. – *Cryptogamie Bryol.* 24: 181–185.
- Goldberg, D. E. and Werner, P. A. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. – *Am. J. Bot.* 70: 1098–1104.
- Hanski, I. 1998. Metapopulation dynamics. – *Nature* 396: 41–49.
- Hanslin, H. M., Bakken, S. and Pedersen, B. 2001. The impact of watering regime and ambient relative humidity on the effect of density on growth in two boreal forest mosses, *Dicranum majus* and *Rhytidiadelphus loreus*. – *J. Bryol.* 23: 43–54.
- Hardin, G. 1968. The tragedy of the commons. – *Science* 162: 1243–1248.
- Hassel, K., Pedersen, B. and Söderström, L. 2005. Age and size at maturity in mountain and lowland populations of the expanding moss *Pogonatum dentatum*. – *Plant Ecol.* 179: 207–216.
- Hedenäs, H., Bolyukh, V. O. and Jonson, B. G. 2003. Spatial distribution of epiphytes on *Populus tremula* in relation to dispersal mode. – *J. Veg. Sci.* 14: 233–242.
- Herben, T. and Söderström, L. 1992. Which habitat parameters are most important for the persistence of a bryophyte species on patchy, temporary substrates. – *Biol. Conserv.* 59: 121–126.
- Herben, T., Rydin, H. and Söderström, L. 1991. Spore establishment probability and the persistence of the fugitive invading moss, *Orthodontium lineare*: a spatial simulation model. – *Oikos* 60: 215–221.
- Hietz, P. 1997. Population dynamics of epiphytes in a Mexican humid montane forest. – *J. Ecol.* 85: 767–775.
- Hobbs, V. J. and Pritchard, N. M. 1987. Population dynamics of the moss *Polytrichum piliferum* in north-east Scotland. – *J. Ecol.* 75: 177–192.
- Hock, Z., Szövényi, P. and Tóth, Z. 2004. Seasonal variation in the bryophyte diaspore bank of open grasslands on dolomite rock. – *J. Bryol.* 26: 285–92.
- Ignatov, M. and Ignatova, E. A. 2001. On the zoochory of *Schistostega pennata* (Schistostegaceae, Musci). – *Arctoa* 10: 83–96.
- Jonsson, B. G. and Söderström, L. 1988. Growth and reproduction in the leafy hepatic *Ptilidium pulcherrimum* (G. Web.) Vainio during a 4-year period. – *J. Bryol.* 15: 315–325.
- Kimmerer, R. W. and Driscoll, M. J. L. 2001. Bryophyte species richness on insular boulder habitats: the effect of area, isolation, and microsite diversity. – *Bryologist* 103: 748–756.
- Kimmerer, R. W. and Young, C. C. 1995. The role of slugs in dispersal of the asexual propagules of *Dicranum flagellare*. – *Bryologist* 98: 149–153.
- Koponen, A. 1990. Entomophily in the Splachnaceae. – *Bot. J. Linn. Soc.* 104: 115–127.
- Kruys, N., Jonsson, B. G. and Ståhl, G. 2002. A stage-based matrix model for decay-class dynamics of woody debris. – *Ecol. Appl.* 12: 773–781.
- Laaka-Lindberg, S., Korpelainen, H. and Pohjamo, M. 2003. Dispersal of asexual propagules in bryophytes. – *J. Hattori Bot. Lab.* 93: 319–330.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – *Bull. Entomol. Soc. Am.* 15: 237–240.
- Lloret, F. 1991. Population dynamics of the coprophilous moss *Tayloria tenuis* in a Pyrenean forest. – *Holarct. Ecol.* 14: 1–8.
- Marino, P. C. 1997. Competition, dispersal and coexistence of Splachnaceae in patchy habitats. – *Adv. Bryol.* 6: 241–263.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. – Cambridge Univ. Press.
- Maynard Smith, J. and Price, G. R. 1973. The logic of animal conflict. – *Nature* 246: 15–18.
- McLetchie, D. M. and Puterbaugh, M. N. 2000. Population sex ratios, sex-specific clonal traits and tradeoffs among these traits in the clonal liverwort, *Marchantia inflexa*. – *Oikos* 90: 227–237.
- McLetchie, D. N., García-Ramos, G. and Crowley, P. H.

2002. Local sex-ratio dynamics: a model for the dioecious liverwort *Marchantia inflexa*. – *Evol. Ecol.* 15: 231–254.
- Miles, C. J. and Longton, R. E. 1990. The role of spores in reproduction in mosses. – *Bot. J. Linn. Soc.* 104: 149–173.
- Miles, C. J. and Longton, R. E. 1992. Deposition of moss spores in relation to distance from parent gametophytes. – *J. Bryol.* 17: 355–368.
- Mulder, C. P. H., Uliassi, D. D. and Doak, D. F. 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. – *Proc. Natl Acad. Sci.* 98: 6704–6708.
- Økland, R. H. 1995. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. I. Demography. – *J. Ecol.* 83: 697–712.
- Økland, R. H. 1997. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. III. Six-year demographic variation in two areas. – *Lindbergia* 22: 49–68.
- Økland, R. H. 2000. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 5. Consequences of the vertical position of individual shoot segments. – *Oikos* 88: 449–469.
- Økland, R. H. and Økland, T. 1996. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. II. Effects of density. – *J. Ecol.* 84: 63–69.
- Pedersen, B., Hanslin, H. M. and Bakken, S. 2001. Testing for positive density-dependent performance in four bryophyte species. – *Ecology* 82: 70–88.
- Pharo, E. J., Lindenmayer, D. B. and Taws, N. 2004. The effects of large-scale fragmentation on bryophytes in temperate forests. – *J. Appl. Ecol.* 41: 910–921.
- Pohjamo, M. and Laaka-Lindberg, S. 2003. Reproductive modes in the epixylic hepatic *Anastrophyllum hellerianum*. – *Persp. Plant Ecol. Evol. Syst.* 6: 159–168.
- Pohjamo, M. and Laaka-Lindberg, S. 2004. Demographic population structure of a leafy epixylic hepatic *Anastrophyllum hellerianum* (Nees ex Lindenb.) R. M. Schust. – *Plant Ecol.* 173: 73–81.
- Pohjamo, M., Laaka-Lindberg, S., Ovaskainen, O. et al. 2006. Dispersal potential of spores and asexual propagules in the epixylic hepatic *Anastrophyllum hellerianum*. – *Evol. Ecol.* 20: 415–430.
- Proctor, M. C. F. 1980. Diffusion resistances in bryophytes. – In: Grace, J., Ford, E. D. and Jarvis, P. G. (eds), *Plants and their atmospheric environment*. Blackwell, pp. 219–229.
- Read, D. J., Duckett, J. G., Francis, R. et al. 2000. Symbiotic fungal associations in 'lower' land plants. – *Philos. Trans. R. Soc. Lond. B* 355: 815–831.
- Reichard, H. W. 1860. Über das Alter der Laubmoose. – *Verh. Zool. Bot. Ges. Wien* 10: 589–598.
- Rice, S. K., Collins, D. and Anderson, A. M. 2001. Functional significance of variation in bryophyte canopy structure. – *Am. J. Bot.* 88: 1568–1576.
- Rice, S. K., Gutman, C. and Krouglicof, N. 2005. Laser scanning reveals bryophyte canopy structure. – *New Phytol.* 166: 695–704.
- Riechert, S. E. and Hammerstein, P. 1983. Game theory in the ecological context. – *Annu. Rev. Ecol. Syst.* 14: 377–409.
- Rixen, C. and Mulder, C. P. H. 2005. Improved water retention links high species richness with increased productivity in arctic tundra moss communities. – *Oecologia* 146: 287–299.
- Rydgren, K. and Økland, R. H. 2001. Sporophyte production in the clonal moss *Hylocomium splendens*: the importance of shoot density. – *J. Bryol.* 23: 91–96.
- Rydgren, K. and Økland, R. H. 2002a. Life-cycle graphs and matrix modelling of bryophyte populations. – *Lindbergia* 27: 81–89.
- Rydgren, K. and Økland, R. H. 2002b. Ultimate costs of sporophyte production in the clonal moss *Hylocomium splendens*. – *Ecology* 83: 1573–1579.
- Rydgren, K. and Økland, R. H. 2002c. Sex distribution and sporophyte frequency in a population of the clonal moss, *Hylocomium splendens*. – *J. Bryol.* 24: 207–214.
- Rydgren, K. and Økland, R. H. 2003. Short-term costs of sexual reproduction in the clonal moss *Hylocomium splendens*. – *Bryologist* 106: 212–220.
- Rydgren, K., de Kroon, H., Økland, R. H. et al. 2001. Effects of fine-scale disturbances on the demography and population dynamics of the clonal moss *Hylocomium splendens*. – *J. Ecol.* 89: 395–405.
- Schieving, F. and Poorter, H. 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. – *New Phytol.* 143: 201–211.
- Snäll, T., Ribeiro Jr., P. J. and Rydin, H. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. – *Oikos* 103: 566–578.
- Snäll, T., Fogelqvist, J., Ribeiro Jr., P. J. et al. 2004. Spatial genetic structure in two congeneric epiphytes with different dispersal strategies analysed by three different methods. – *Mol. Ecol.* 13: 2109–2119.
- Snäll, T., Ehrlén, J. and Rydin, H. 2005a. Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. – *Ecology* 86: 106–115.
- Snäll, T., Pennanen, J., Kivistö, L. et al. 2005b. Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. – *Oikos* 109: 209–22.
- Söderström, L. and Daring, H. J. 2005. Bryophyte rarity viewed from the perspectives of life history strategy and metapopulation dynamics. – *J. Bryol.* 27: 261–268.
- Söderström, L. and Herben, T. 1997. Dynamics of bryophyte metapopulations. – *Adv. Bryol.* 6: 205–240.
- Stark, L. 2001. Widespread sporophyte abortion following summer rains in Mojave Desert populations of *Grimmia orbicularis*. – *Bryologist* 104: 115–125.
- Stark, L. 2002. Skipped reproductive cycles and extensive sporophyte abortion in the desert moss *Tortula inermis* correspond to unusual rainfall patterns. – *Can. J. Bot.* 80: 533–542.
- Stark, L. and Delgadillo M. C. 2003. Is *Crossidium crassinerve* (Pottiaceae) an annual moss? Observations on vegetative allocation and viability from Mojave Desert populations. – *Lindbergia* 28: 3–13.
- Stark, L., Mishler, B. D. and McLetchie, D. N. 2000. The cost of realized sexual reproduction: assessing patterns of reproductive allocation and sporophyte abortion in a desert moss. – *Am. J. Bot.* 87: 1599–1608.
- Sundberg, S. 2005. Larger capsules enhance short-range spore dispersal in *Sphagnum*, but what happens further away? – *Oikos* 108: 115–124.
- Sundberg, S. and Rydin, H. 2002. Habitat requirements for establishment of *Sphagnum* from spores. – *J. Ecol.* 90: 268–278.

- Thornber, C. S. and Gaines, S. D. 2004. Population demographics in species with biphasic life cycles. – *Ecology* 85: 1661–74.
- van der Hoeven, E. C. and During, H. J. 1997. Positive and negative interactions in bryophyte populations. – In: de Kroon, H. and van Groenendael, J. (eds), *The ecology and evolution of clonal plants*. Backhuys Publishers, pp. 291–310.
- van der Velde, M., During, H. J., van der Zande, L. et al. 2001. The reproductive biology of *Polytrichum formosum*: clonal structure and paternity revealed by microsatellites. – *Mol. Ecol.* 10: 2423–2434.
- Verburg, R., Maas, J. and During, H. J. 2000. Clonal diversity in differently aged populations of the pseudo-annual clonal plant *Circaea lutetiana* L. – *Plant Biol.* 2: 646–652.
- Vitt, D. H. 1991. Patterns of growth of the drought tolerant moss, *Racomitrium microcarpon*, over a three year period. – *Lindbergia* 15: 181–187.
- Weibull, H. 2000. Bryophytes on boulders: diversity, habitat preferences and conservation aspects. – PhD thesis, Univ. of Agric. Sc., Uppsala.
- Weibull, H. and Rydin, H. 2005. Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. – *Biol. Conserv.* 122: 71–79.
- Wiklund, K. and Rydin, H. 2004. Ecophysiological constraints on spore establishment in bryophytes. – *Funct. Ecol.* 18: 907–913.
- Yodzis, P. 1989. *Introduction to theoretical ecology*. – Harper & Row.
- Zartman, C. E. 2003. Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. – *Ecology* 84: 948–954.