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## Review

# Conservation strategies for lichens: insights from population biology

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### ABSTRACT

To design effective conservation strategies, the population biology of the target organism needs to be well understood. In lichens, the population dynamics of the symbiotic organism is closely tied to the dynamics of its substrate. Here, we review the population biology of selected lichens, highlighting the link between landscape and lichen population dynamics. We suggest strategies to efficiently protect lichen species and develop priorities for species conservation approaches.

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## 1. Introduction

Conservation biology aims at maintaining self-sustaining populations of rare and endangered species. This task can be achieved by a combination of strategies that target focal species and habitat conservation measures. Population biology can contribute greatly to the development of appropriate conservation strategies for lichens by understanding and documenting the needs of rare or endangered species in dynamic landscapes (Scheidegger *et al.*, 1997), by identifying the critical stages in the life cycle of the target species (Scheidegger *et al.*, 1995; Sillett *et al.*, 2000; Zoller *et al.*, 2000; Hilmo and Sastad, 2001; Werth *et al.*, 2006a), and by inferring the

distance at which habitats are connected through dispersal (Wagner *et al.*, 2006; Werth *et al.*, 2006a).

It is important to notice that climatic conditions may influence with the life-cycle properties of poikilohydric species and thus change their requirements for habitat quality. For instance, oceanic species tend to be extreme habitat specialists in relatively continental areas, whereas they are rather generalistic in areas with a more moist climate (Goward, 1995; Werth *et al.*, 2005). Therefore, both the conservation of rare and endangered lichen species requires a deep understanding of the ecology of the target species, in a given region. This paper describes the application of population biology to the conservation biology of lichens in dynamic landscapes,

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with a particular focus on the role of life-history traits such as dispersal or establishment. Moreover, we suggest how such life-history properties can be used for dynamic landscapes in combination with ecological knowledge to design powerful conservation strategies.

Symbiotic organisms such as lichens are not an easy target for conservation measures, especially if the interactions between the symbionts are ecologically obligately biotrophic. A lichen is a stable, self-supporting association of a fungus (exhabitant) (Kirk *et al.*, 2008) and one or more algal and/or cyanobacterial photobionts. While the conservation biology of lichens deals with more than one organism, in practice the symbiotic phenotype, which is named after the mycobiont, is the main focus of conservation (Scheidegger and Goward, 2002). Lichen-forming fungi often have specific habitat requirements which are not generally shared by other organisms, and lichens are usually not considered when reserves are designed. Therefore, an ecosystem approach of conservation rarely leads to successful results in these inconspicuous organisms.

The main threats that apply to biodiversity in general are also true for lichens, e.g. habitat degradation and loss (Groom *et al.*, 2006), habitat fragmentation (Bergamini *et al.*, 2005), overexploitation (Upreti *et al.*, 2005), species invasions (La Greca and Stutzman, 2006), and climate change. For instance, climate change is likely to have dramatic effects on distribution and abundance of lichen populations (Ellis and Coppins, 2007; Ellis *et al.*, 2007). Overbrowsing of the *Cladonia* heath by increasing reindeer populations in Scandinavia and Alaska has long been recognised as an important factor causing the severe decline of lichens, which might become a serious problem in reindeer husbandry (Suominen and Olfosson, 2000). Yet another threat which is specific to lichens and other poikilohydric cryptogams is air pollution, which has led to the severe decline of numerous species throughout Central Europe (Nimis *et al.*, 2002). In the following, we give some examples for threats to lichens and we illustrate in which cases an understanding of population biology could help to amend these threats.

Overexploitation of lichen populations for human uses is a serious problem, even if the demand is not increasing, but the size or quality of the habitat is declining. Upreti *et al.* (2005) report an overexploitation of epiphytic macrolichens in the Himalayas because of a declining forest area. These lichens grow abundantly in the mountain forests and were traditionally harvested to cover the national demand of spices and perfumes (Upreti *et al.*, 2005). Although the harvested species are common and locally abundant in these forests, the immediate threat is that an overexploitation of this resource will lead to a decline of the population density. This, in turn, can lead to a reduced propagule source and, as a consequence, a lower rate of recruitment. The productivity of the lichen community is reduced while the demand for the resource remains constant. Because these lichens are an important part in the cultural life of a large human population, increasing market prices will in all likelihood not regulate the demand for this resource. However, the major concern with this example is that rare species co-occurring with commonly harvested target species will be threatened even more ("bycatch"). In this particular case, mitigative measures



**Fig. 1 – *Lobaria pulmonaria* is a widespread but regionally threatened foliose lichen. This species is used for medicinal purposes, in many regions it is an indicator species for natural forest landscapes and it is widely used as a model species in ecophysiological, ecological and conservation biological research.**

should focus on habitat protection and the regulation of collections; a species-based approach is unlikely to be helpful because whole communities are harvested in this example.

The use of lichens for medicinal purposes is generally more specific to selected species such as *Cetraria islandica* or *Lobaria pulmonaria* (Fig. 1). Because the price for this biological resource is generally high, small and vulnerable populations can also be exploited in an economically profitable way. In this case, harvesting could negatively affect the long-term survival of populations, if a major part of a regional population is not kept within the borders of protected areas. However, partial harvest of *L. pulmonaria* thalli recently proved to be an economically profitable and sustainable method to collect material of this regionally rare and protected species. With this approach, a minimum of 15 trees that are colonised with *L. pulmonaria* will remain untouched, on each tree where *L. pulmonaria* is harvested, at least three large thalli will remain unaffected, and from each thallus that will be harvested, the upper portion of the thallus will remain on the tree. Thus, the lobes that have active growth zones will regenerate the harvested part of the thallus. In order to compensate for the reduced number of produced diaspores, small lobes of harvested *L. pulmonaria* thalli have to be transplanted on a minimum of four trees that are still uncolonized (Scheidegger *et al.*, 2007).

Habitat degradation and loss is the most serious threat to biodiversity in general (Groom *et al.*, 2006) and in lichens in particular (Wirth, 1976, 1999). Loss of habitat leads to a reduction of local population sizes, and saxicolous, terricolous and epiphytic species are all similarly affected. Habitat loss has been identified as the most widespread threat to lichens, clear-cuts of old or natural forests accounting for 63 % of lost sites (Wolseley, 1995). Deforestation and degradation of lichen habitats by the replacement of natural forests with plantation forests have both a drastic effect on species richness and composition of lichen communities (Rose, 1992). This was

also found across a continental gradient that included different bioclimatic regions (Bergamini *et al.*, 2005; Stofer *et al.*, 2006). Natural forests were found to host a characteristic lichen flora that is not found in secondary forests or fragmented forest landscapes (Bergamini *et al.*, 2005). Old-growth dependency of lichens has been documented in deciduous woodlands (Rose, 1976; Rose, 1992) and forests (Tibell, 1992; Goward, 1994; Selva, 1994; Goward, 1995), including tropical regions (Plata *et al.*, 2008). Some species depend on habitats and moisture regimes characteristic for old trees. As extreme habitat specialists, many calicioid lichens grow exclusively in bark crevices that only veteran trees can provide (Selva, 1994). Dispersal limitation has been discussed as an alternative explanation for the restriction of species to old-growth forests (Scheidegger, 1995; Sillett *et al.*, 2000; Hilmo and Sastad, 2001). Although this is a well-known phenomenon with many other lichens such as *Usnea longissima*, *L. pulmonaria* and associated species, the ecological basis of the strong association of these species to old-growth habitats is not yet fully understood. Gu *et al.* (2001) explained a reduced frequency of *L. pulmonaria* in managed forests with the disruption of habitat continuity in the latter. The old-growth dependency of species may also vary along ecological gradients. Along a climate gradient from oceanic to humid continental, *Nephroma occulatum* changes not only its vertical distribution in the forest canopy but also reveals an increasing dependency on old-growth stands (Goward, 1995). Old-growth dependent species, which require particular habitat conditions in continental climates where establishment takes longer, may be able to grow on a multitude of substrates in oceanic climates (Goward, 1994; Werth, 2001; Werth *et al.*, 2005). One explanation is that a beneficial microclimate may increase recruitment rates and lower substrate specificity. This hypothesis would have to be tested with reciprocal transplant experiments of lichen propagules (Scheidegger, 1995) to oceanic and continental areas, followed by studies on their establishment and juvenile development. Also, investigating growth rates of fragments of adult lichen thalli, reciprocally transplanted to continental and oceanic sites, can help to shed some light on this issue (Hallingbäck, 1990; Scheidegger *et al.*, 1995; Walser and Scheidegger, 2002; Werth *et al.*, 2006a). However, one concern is that survival and growth of adults may reveal little about recruitment success, which may be the decisive factor for lichen population dynamics. Therefore, a detailed study of population biological properties, including, but not limited to juvenile development and dispersal, may help to identify at which stage in the life cycle of these lichens an immediate threat exists.

Several of the examples in our review draw on our work with the epiphytic lichen *L. pulmonaria* (Fig. 1). We have used this species as a model organism because i) it is not yet too rare to initiate strategies for its protection; ii) one of the threats for this species are forest management strategies which do not take into account epiphytic species with long generation times; iii) it is associated with a variety of other even more rare or more endangered lichens that share its habitat requirements, have a similar life history (e.g. species of the genera, *Sticta*, *Degelia*, *Collema*); and iv) *L. pulmonaria* can be considered a flagship and umbrella species for these. Here, we review the population biology of lichens, with



**Fig. 2 – *Erioderma pedicellatum* is a critically endangered cyanobacterial lichen species.**

a particular emphasis on the link between lichen and landscape dynamics, and we summarise the implications for conservation.

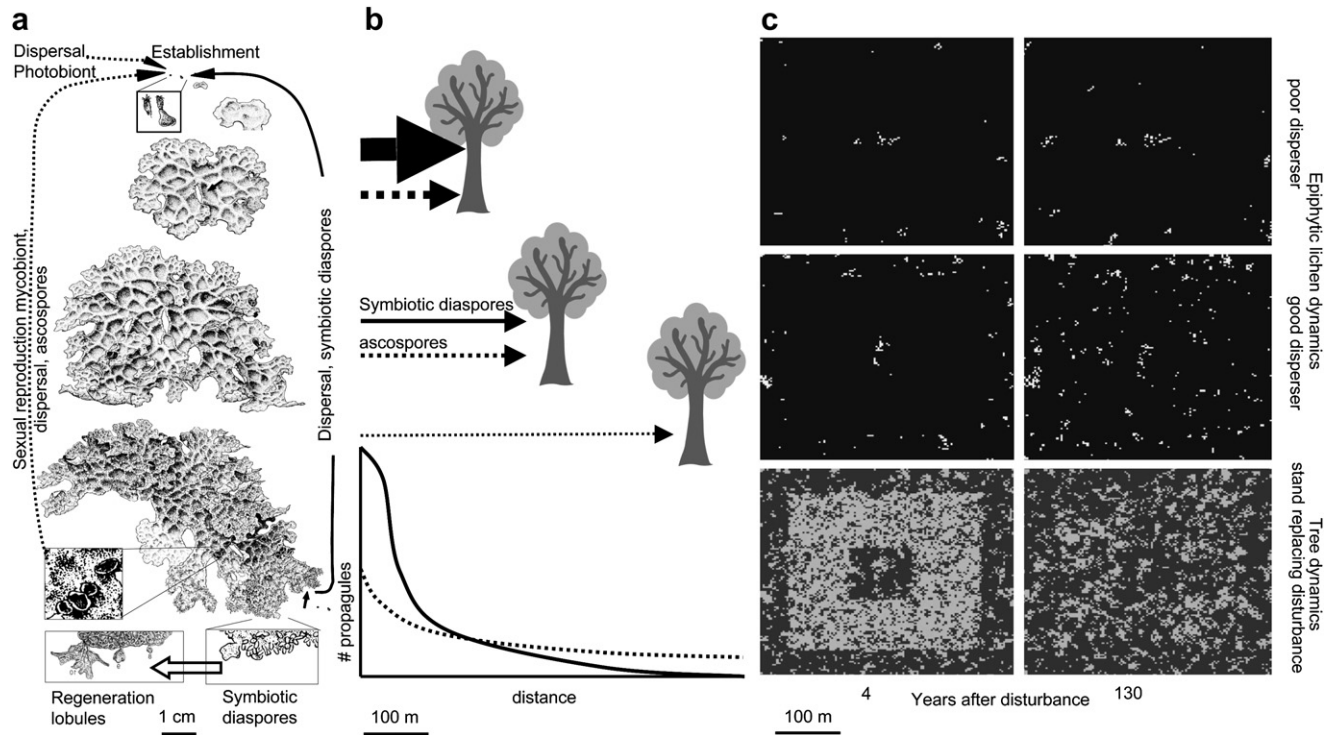
## 2. Population Biology of lichens

Detailed demographic investigations that include all life-stages are still largely missing for lichen populations. Such data are urgently needed for detailed analyses of the continuous decline of populations of threatened species in presumably intact habitats such as the globally threatened epiphytic species *Erioderma pedicellatum* (Fig. 2) in the mixed balsam fir and spruce forests of Newfoundland (Scheidegger, 1998).

### Reproduction

Lichens reveal various reproductive strategies where the mycobiont and its photobionts either disperse separately, in the case of sexual reproduction (horizontal transmission of photobionts) or where the lichen symbionts are codispersed with clonal, symbiotic propagules (vertical transmission of photobionts; Yahr *et al.*, 2004). With a few exceptions, where photobionts grow between the meiosporangia of the mycobiont and are codispersed with the ascospores (Ahmadjian, 1993), sexual reproduction is always associated with horizontal transfer of photobionts. In many fruticose lichen species, thalli can break apart after mechanical stress from trampling, wind, water or snow, and clonal fragments can subsequently form new thalli if dispersed to a safe site. A high number of species develop symbiotic propagule types such as isidia or soredia that facilitate clonal reproduction of the symbiosis (Büdel and Scheidegger, 2008). In many species, these diaspores are multifunctional and can develop into regeneration structures (Ott *et al.*, 1993). Species with a predominantly clonal reproductive mode can exhibit extensive clonal genetic structure (Walser *et al.*, 2004, 2005; Wagner *et al.*, 2005; Werth *et al.*, 2006b) (Fig. 3). Some predominantly sexually reproducing lichen fungi may lack any structure at the local scale (Werth and Sork, 2008).





**Fig. 3 – (a) Life cycle of *Lobaria pulmonaria*. Photobiont cells and ascospores or symbiotic diaspores adhere, attach and develop into stratified, juvenile thalli (establishment). During more than a decade the thalli grow and form symbiotic and under favourable conditions later also sexual diaspores. Symbiotic diaspores can also develop into regeneration lobes if not detached from the thallus. (b) Dispersal distances of sexual and clonal, symbiotic diaspores of *Lobaria pulmonaria*. At short dispersal distances symbiotic diaspores prevail but sexual diaspores are better adapted to larger dispersal distances. (c) Simulation experiment of stand-level recolonisation of an epiphytic lichen (bright spots) with short (above) and high (middle) dispersal range after a stand-replacing disturbance event (with a remaining island in the middle of the quadrat) in a mixed forest with coniferous (dark spots) and deciduous (bright spots) trees (below). The lichen only grows on the deciduous tree species, which are more frequent in early stages of the forest succession. The epiphytic species with a high dispersal range can recolonise the stand within one tree generation after a stand-replacing disturbance event, whereas the species with poor dispersal potential remains limited to the non-disturbed parts of the forest landscape. More than one tree generation is needed for the species with short dispersal range to recolonise a newly established forest stand. Adapted after Scheidegger et al., 1997; Werth et al., 2006a; Wagner et al., 2006).**

Sexual reproduction in lichens refers specifically to the sexuality of the lichen-forming fungus. During fungal sexual reproduction, ascospores are formed in ascocmata (Ascomycetes) or, in basidiolichens, basidiospores are formed. Some lichen-forming fungi are capable of both selfing and outcrossing (homothallism), while others are obligatory outcrossers (heterothallism) (Zoller et al., 1999; Murtagh et al., 2000; Honegger et al., 2004; Scherrer et al., 2005; Honegger and Zippler, 2007; Honegger and Scherrer, 2008). In heterothallic species, the lack of a compatible partner precludes sexual reproduction. This situation might occur predominantly in small populations, populations that have gone through genetic bottlenecks during extended time periods with small population sizes, or newly founded populations.

Many lichens have a mixed reproductive mode that includes clonal reproduction through clonal, symbiotic propagules and, additionally, some sexual reproduction (Fig. 3a). This combined strategy appears to be particularly beneficial in relatively undisturbed habitats in which there is a low

intensity of biotic interactions because it perpetuates successful genotypes adapted to the prevailing environmental regimes. If a genotype is locally well adapted to its environment, clonal reproduction will result in fit offspring. Also, the risks of relichenisation (i.e. whether a sporeling will meet a compatible photobiont) are reduced by production of clonal, symbiotic propagules. Vertical transmission may therefore be a good strategy allowing lichens to persist, as long as environmental conditions do not change. However, in a fluctuating environment, it might be disadvantageous to maintain a symbiont of a single strain through generations compared to hosts changing symbionts among various strains (Genkai-Kato and Yamamura, 1999). Symbiotic variation, i.e. the variation between symbiont genotypic patterns (Robertson and Piercey-Normore, 2007) as well as genetic variation of both symbionts are assumed to be important for a symbiosis and its symbionts to adapt to new habitats. Symbiotic variation depends on compatibility of the symbionts (Honegger, 2008) and can result from a combination of clonality and

juvenile development from ascospores involving horizontal transmission of photobiont partners between fungi (Robertson and Piercey-Normore, 2007).

Although recombined symbionts, and offspring that reveal symbiotic variation, can be maladapted to local conditions, there is also a slight chance that they be better adapted than their parents and thus, sexual reproduction coupled with horizontal transmission of photobionts can be an advantage, particularly in unpredictable (Maynard Smith, 1978) and abiotically extreme environments (Murtagh et al., 2000; Seymour et al., 2005).

Some lichen-forming fungal species exhibit contrasting reproductive strategies in different parts of their ranges (Poelt, 1970, 1972; Tehler, 1982; Mattsson and Lumbsch, 1989; Lohtander et al., 1998; Kroken and Taylor, 2001, Cornejo et al., 2009). Often, due to their different reproductive mode, these were described as separate species, when in fact they are conspecific. One example of these so-called “species pairs” is the sexual lichen *Porpidia flavocoerulescens* and its clonal counterpart, *P. melinodes* (Buschbom and Mueller, 2006).

### Dispersal

Dispersal is a fundamental process in the life history of lichens (Bailey, 1976). Successful dispersal is the precondition for new habitats to be occupied, for habitat patches of a meta-population to get colonised and for new populations to be founded.

Size of the propagule might be an important determinant of the characteristic dispersal distance. Indeed, Armstrong (1990) found a much higher dispersal distance of soredia relative to the larger thallus fragments. Microscopic ascospores appear to disperse over much longer distances than any symbiotic propagules (Werth et al., 2006b; Fig. 3b). Heinken (1999) studied the dispersal of marked thallus fragments of seven terricolous lichen species, and found wind dispersal distances shorter than one metre. The largest dispersal distance found in this study was caused by animal dispersal of thallus fragments at a distance of about 10 m.

Some lichens are good dispersers, and can efficiently disperse their propagules across larger distances. Only 3 y after the last phase of volcanic eruption, the new island of Surtsey (Iceland) had already been colonised by three lichen species (Kristinsson, 1972). Marshall (1996) trapped lichen propagules in the maritime Antarctic, and found a predominance of soredia in the samples (depending on the trapping location, 60–80 % of propagules were soredia). Soredia were found at distances of up to 50 m from the nearest potential source. Moreover, several lichens have been shown to re-establish in areas which were formerly known as lichen deserts owing to air pollution (Kandler and Poelt, 1984).

Some lichen species reproducing with large propagules have been suggested to be dispersal limited. In epiphytes, these species are often primarily found in old-growth sites and forests with a low disturbance regime (Dettki et al., 2000; Sillett et al., 2000). Using molecular techniques, Walser et al. (2001) and Werth et al. (2006a) investigated the deposition of propagules of *L. pulmonaria* around single trees colonised by the species. They found that diaspores were deposited up to 40 or 50 metres

distance from the source, respectively. Additionally, Werth et al. (2006a) also registered a substantial amount of dispersal over larger distances, e.g. at least 200 m (Fig. 3b).

Also simulation models can shed light on the dispersal process. Wagner et al. (2006) simulated the recolonisation of disturbed forests by *L. pulmonaria*, and found that in addition to local dispersal, substantial long-distance dispersal was needed to explain the persistence of the species in the dynamic pasture-woodland landscape with its contemporary levels of genetic variability (Fig. 3c).

For dispersal to be successful, a sufficiently large propagule pool is needed. For instance, the recolonisation of heavily polluted urban areas by common lichen species sensitive to air pollution can vary greatly among species (Gilbert, 1992) but may take decades because the founding populations are small, propagules must travel over large distances, or there may be low levels of propagule production. Also in rare species with small population sizes, the propagule pool can be depleted so that dispersal might become a factor limiting persistence in managed and dynamic landscapes (Wagner et al., 2006; Werth et al., 2006a).

It is important to notice that studies dealing with young or adult thalli cannot draw conclusions on dispersal *per se* (c.f. Tapper, 1976; Walser, 2004; Öckinger et al., 2005), because only successfully established juveniles are recognised – these studies measure the combined effect of dispersal and establishment (i.e., effective dispersal). In species with low establishment rates, most dispersal events will go unrecognised if established lichen thalli are investigated. Studying established thalli, dispersal and establishment can not be disentangled (Werth et al., 2006a), and this may lead to wrong conclusions as of whether dispersal or establishment is the limiting factor for colonisation. Nevertheless, Öckinger et al. (2005) studied the colonisation of trees by *L. pulmonaria* nine years after an initial survey had been performed; an average effective dispersal distance of 35 m and a maximum of 75 m were recorded. They also found an effect of habitat quality – trees colonised by *L. pulmonaria* differed from control trees by a larger circumference and a higher bryophyte cover (Öckinger et al., 2005).

### Establishment and juvenile development

Critical stages in the life cycle of a lichen are the establishment of a thallus from a propagule (Bailey, 1976) and the following phase, juvenile development. The former starts after dispersal when the diaspore contacts the substrate and ends when the diaspore first reveals the species' characteristics such as secondary compounds, thallus stratification and attachment organs. Later a juvenile develops into an adult thallus as it starts reproducing, either clonally or sexually.

After dispersal, propagules need to adhere to the substrate. Adhesion, an entirely physical process, is decisive for the fate of an individual propagule. If not able to adhere immediately, a propagule may just drop or be washed off its substrate. Moreover, during desiccation and rehydration cycles, adhering propagules can easily drop or be washed off the surface (Scheidtger, 1995; Zoller et al., 2000). High rates of loss continue until growing hyphae actively attach the propagules to the substrate. The second phase of a propagule starting to grow is therefore to

spend a considerable growth effort on its attachment – this involves hyphae growing out laterally from the propagule and fixing it to the substrate. In *Sticta sylvatica* and *L. pulmonaria*, attachment can take several months (Scheidegger, 1995; Zoller et al., 2000), although attachment within the first month after sowing of diaspores was reported for *Platismatia glauca*, *P. norvegica* and *Lobaria scrobiculata*, three species with an otherwise slow juvenile development (Hilmo and Ott, 2002). The third key factor for diaspore development is the site where the diaspores attach, relative to the species' ecological niche. Propagules require particular microsites ("safe sites") (Harper, 1977) for their establishment, and often also a beneficial microclimate (Schuster, 1985; Ott, 1987a, b, c, 2004). The rarity of beneficial microsites could seriously limit recruitment – even in species with sufficiently high dispersal ability such as some rare and endangered calicioid lichen species depending on deep bark crevices of veteran deciduous trees.

Fourth, the presence of competitors or herbivores at a microsite is a major mortality factor. An establishing propagule might get outcompeted by faster growing lichens, bryophytes, or phanerogams. Also, particularly the tiny establishing propagules could be especially susceptible to mortality due to grazing by herbivores such as slugs or other invertebrates (Scheidegger, 1995; Zoller et al., 2000; Asplund and Gauslaa, 2008).

Fifth, in lichen-forming fungi with a sexual reproductive mode, there is yet another factor which is decisive for the outcome of the establishment process. In order to establish, germinated ascospores ("sporelings") need to obtain a compatible photobiont and establish the symbiosis, a process called relichenisation (Ahmadjian, 1993). Depending on the fungal species, either green algae or cyanobacteria are required for successful establishment. Rather little is known about the highly interesting "relichenisation" phase of the lichen life cycle (Honegger, 2008). In a molecular community-level study of lichen photobionts, Beck et al. (2002) found evidence for relichenisation in *Fulgensia fulgida*. Werth and Sork (2008) found high genetic variability in *Ramalina menziesii* collected across a landscape and little evidence for clonality. Multiple green algal haplotypes associated with the same multilocus genotype of *R. menziesii*. The results indicated that the lichen-forming fungus was predominantly reproducing sexually through ascospores, involving relichenisations (Werth and Sork, 2008). It is yet uncertain how long a sporeling can survive without having incorporated algae or cyanobacteria, but this would be very interesting to know in the context of population dynamics. The longer a species' sporelings are able to survive by themselves, the larger might be the chance that they will eventually obtain a suitable photobiont, leading to a higher overall establishment success. It has been suggested that photobiont availability might be limiting establishment (Werth et al., 2006a), but it is as of yet unclear whether some groups of lichen-forming fungi have abundant access to photobionts while others do not (Beck et al., 1998). Despite the reportedly high fungal specificity and selectivity for algal symbionts (Yahr et al., 2004; Honegger, 2008), the role of photobiont limitation in relichenisation and population dynamics requires further clarification.

Establishment, i.e. the post-dispersal processes that involve adhesion, attachment and morphogenesis to a juvenile, often

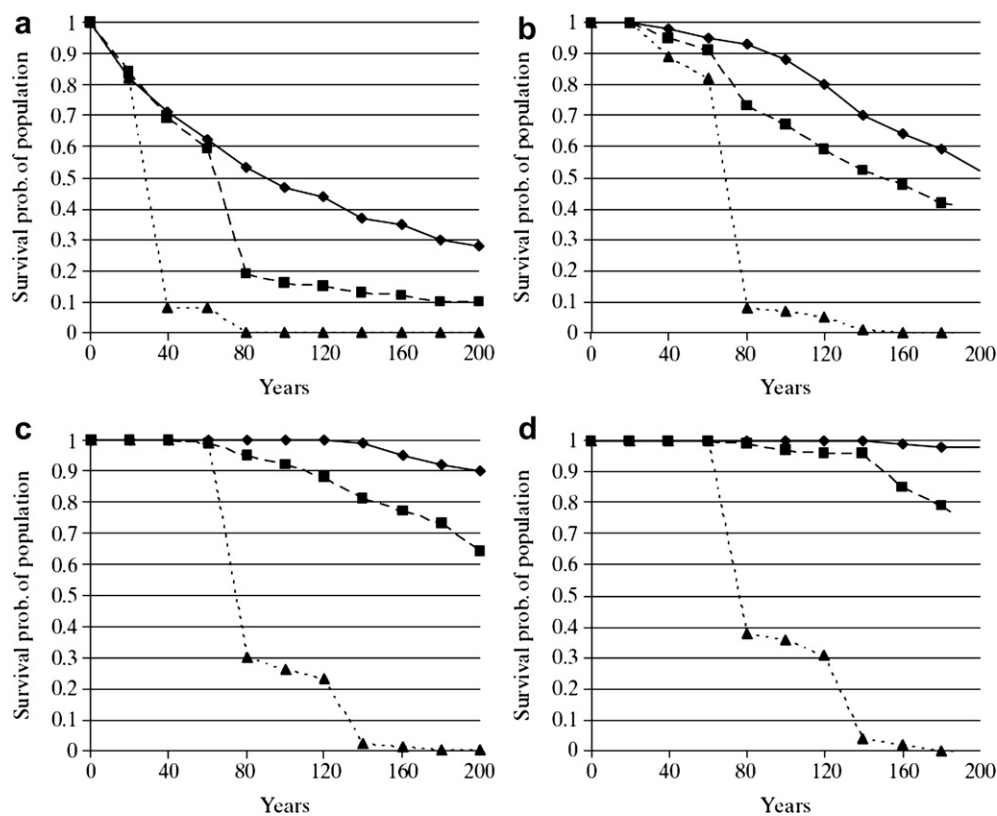
stratified thallus that shows chemical and physiological properties of an adult thallus, is equally important as dispersal for a species to be successful at colonising new sites and for its long-term persistence. If dispersal is efficient, but establishment rates are low, recruitment is reduced, leading for instance to the inability to colonise new sites. If the habitat is dynamic like a tree population, and is suitable only for a certain time, the time frame available for colonisation is limited. If establishment rates are low, and rotation cycles are short, an epiphytic lichen species may not manage to fulfil its life cycle, hindering its long-term persistence of populations.

### 3. Lichen population biology in dynamic landscapes

The single most important cause of death for epiphytic lichens in the case of late successional, competitive epiphytic species is the death of their substrate, i.e. the host tree that is often referred to as phorophyte to stress the lack of nutritional interactions between lichen and tree. Therefore, all conspecific thalli inhabiting a tree individual, can, for practical purposes, be considered a functional individual (Scheidegger and Goward, 2002), which has to be distinguished from genets or ramets (Harper, 1977). This approach makes population studies of epiphytic lichens easy because the mortality of the lichen functional individual can be related to the mortality of the host tree (Scheidegger et al., 2000).

Based on this concept, an individual-based, spatially implicit stochastic simulation model was developed for *L. pulmonaria* in an upper montane mixed forest and used to estimate the local extinction probability of small populations (Scheidegger et al., 1998). Under a scenario of a natural forest dynamics, i.e. when a tree's age is only limited by an average yearly mortality, the survival probability of local populations of *L. pulmonaria* strongly depends on the number of functional individuals at the beginning of the simulation. With only one functional individual the simulations reveal a rapid decrease in the population's survival probability to 47 % and 30 % after 100 and 200 y, respectively (Fig. 4a). With four, 10 and 15 functional individuals at the beginning of the simulation period, the survival probabilities over 200 y increase from 50 % to 90 % and 97 %, respectively and populations that consist of 10 trees and more can therefore be regarded as robust against the stochastic events considered in these simulations (Fig. 4b–d). However, forest management may severely reduce the survival probability of small populations, as revealed by the simulation experiments. What is considered a sustainable level of tree harvest from a forest management perspective, will inevitably lead to the extirpation of *L. pulmonaria* populations, even in stands with 15 functional individuals (Scheidegger et al., 1998). Even low levels of tree harvest considerably increase the vulnerability of small populations, although the decline is much reduced in larger populations (Scheidegger et al., 2000).

In a recent project, we studied the effects of landscape dynamics on population size and genetic structure of a population of *L. pulmonaria* in a traditionally managed pasture-woodland landscape in the Jura Mountains of Switzerland. The high biodiversity and conservation value of this traditionally



**Fig. 4 – Survival probabilities of *Lobaria pulmonaria* populations over 200 y. ◆ No harvest; ■ 50 % of mature trees are not harvested; 25 % harvest after 40, 80, 120 and 180 y; ▲ rotation cycle 90 y; 50 % harvest after 40 and 80 y. Population consists of a) 1 tree; b) 4 trees; c), 10 trees and d) 15 trees colonised with *Lobaria* at the beginning of the simulation (after Scheidegger et al., 2000).**

managed pasture-woodland landscape is largely the result of a variety of different types of disturbance, with varying intensities and spatial extents, from the tree to the forest-stand level. These include grazing, different intensities of forest management and stand-replacing disturbance, events caused by blow-downs and severe forest fires, one from 1871 being well documented. An analysis of variance of the *L. pulmonaria* population density showed that neither historical stand-level disturbances nor current grazing reduced the proportion of occupied trees. Spatial analysis at the tree level revealed a patchy distribution of occupied trees, suggesting *L. pulmonaria* colonisation from nearby sources. Spatial analysis at the 1 ha plot level even showed a positive spatial association of *L. pulmonaria* with historic disturbances, probably because the host tree of *L. pulmonaria*, *Acer pseudoplatanus* reached a higher density following disturbance such as intensive forest management for charcoal production (Kalwij et al., 2005).

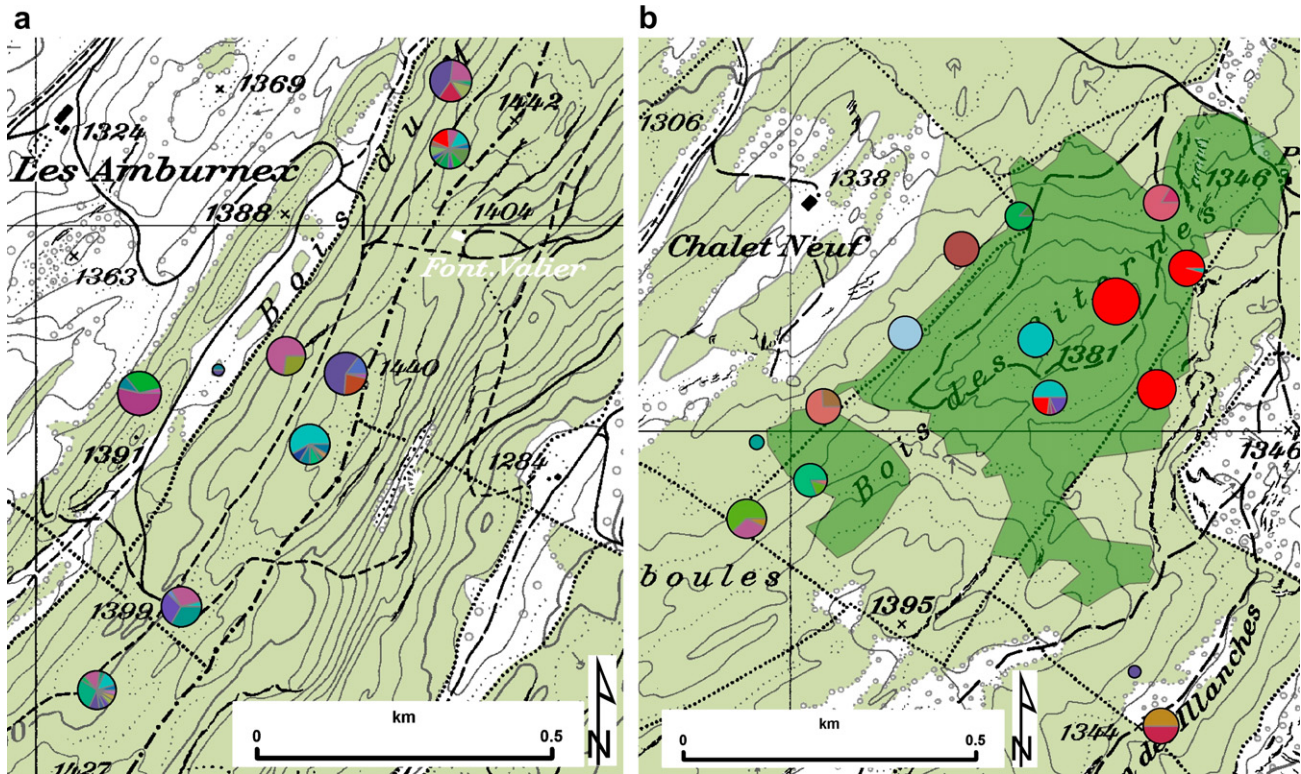
Based on molecular analyses of fungus-specific, neutral microsatellite markers (Walser et al., 2003), Werth et al. (2006b) found evidence for multiple independent colonisations of plots that were traditionally managed under uneven-aged forestry (Fig. 5a). However, population-genetic data suggested that after stand-replacing disturbance, each plot was colonised by only one to few genotypes, which subsequently spread clonally within a local neighbourhood (Fig. 5b). Spatial autocorrelation of genotype diversity was strong at short distances up to

50 m in logged demes, up to 100 m in uneven-aged demes, with the strongest autocorrelation up to 150 m for burnt demes. This clearly shows that the type of forest stand can influence typical dispersal distances of a wind-dispersed lichen species. The spatial autocorrelation was predominantly attributed to clonal dispersal of vegetative propagules. After accounting for the clonal component, Werth et al. (2006b) did not find significant spatial autocorrelation in gene diversity. This pattern may indicate low dispersal ranges of clonal propagules, but random dispersal of sexual ascospores.

Genetic diversity was highest in logged demes, and lowest in burnt demes. These results suggest that the genetic diversity of epiphytic lichen demes may not necessarily be impacted by stand-level disturbances for extended time periods (Werth et al., 2006b). However, stand-replacing events that interrupt the overlap of tree generations and thus lead to local extinction of *L. pulmonaria* may have a strong and long-lasting negative effect on genetic diversity of a regenerating population, and population density may increase while genetic diversity remains low.

Within the study region, Werth et al. (2007) found significant isolation by distance for *L. pulmonaria* demes, and significant genetic differentiation among sampling plots and among trees. There was no traceable pattern in genetic structure of the population of *L. pulmonaria* between two forested regions that were separated by a large meadow, presumably of medieval origin. Gene pools were spatially intermingled





**Fig. 5** – Spatial distribution of fungal three-locus genotypes in *Lobaria pulmonaria*, collected in 1-ha plots in a pasture-woodland landscape in western Switzerland. The microsatellite markers used were LPu03, LPu09, and LPu15. The segments of the pie charts indicate the frequency of each multilocus genotype in a plot, where chart size is proportional to the sample size. a) Area under uneven-aged forestry; b) area burnt in 1871, affected by a stand-replacing event. The illustration shows extensive sharing of three-locus genotypes in the burnt area (b), whereas in the uneven-aged forest, a higher number of genotypes were found per each plot and few genotypes were shared among plots (a).

across the pasture-woodland landscape, as determined by Bayesian analysis of population structure. Evidence for local gene flow was found in a disturbed area that appeared to have mainly been colonised from nearby sources. The low genetic differentiation of *L. pulmonaria* among forest regions may reflect the historical connectedness of the landscape through gene movement. Altogether, these results support the conclusion that dispersal in *L. pulmonaria* is rather effective, but not spatially unrestricted (Werth et al., 2007).

Because the historical connectedness of the landscape had been changed by anthropogenic influences such as the opening of large meadows, only the study of current gene flow and dispersal range can reveal whether the studied demes of *L. pulmonaria* are still functionally connected in today's landscape. Werth et al. (2006a) analyzed 240 snow samples that were collected across a landscape with real-time PCR of ITS and detected propagules not only in forests where *L. pulmonaria* was present, but also in large unforested pasture areas, and in forest patches where *L. pulmonaria* was not found. The results indicated functional connectivity of the landscape for this lichen.

Monitoring of soredia of *L. pulmonaria* after two vegetation periods after transplantation to maple bark showed high variance in growth among forest stands, but no significant differences among different transplantation treatments. Hence, in

what is probably the largest *L. pulmonaria* population in Switzerland, it appears that ecological constraints at the stand level, rather than dispersal is important and limits colonisation (Werth et al., 2006a).

Wagner et al. (2006) developed a model to compare the spatial distribution and genetic structure of *L. pulmonaria* within an area of a reconstructed 19th century disturbance and a nearby reference area without stand-level disturbance (see Figs 3c, 5). Although model calibration suggested a predominance of dispersal from local clonal propagules, a substantial contribution of immigration of non-local genotypes by long-distance dispersal was needed to reach the observed levels of genotype diversity (Wagner et al., 2006).

The persistence of *L. pulmonaria* in the studied dynamic pasture-woodland landscape therefore depended on complex interactions between the spatial distribution, abundance and genetic diversity of populations, and the type, spatial extent, frequency and severity of disturbance of the lichen habitat. Large and luxuriant populations are likely to have considerably higher levels of resilience than small populations, especially to stand-level disturbance events. Furthermore, it is likely that microscopic sexual propagules play an important role in the colonisation process after stand-level disturbance events (Fig. 3b).

In the case of single, isolated populations, those with sexually reproducing individuals should therefore be given a higher



rank in terms of conservation priority than strictly asexual populations (Zoller *et al.*, 1999). At the landscape level, vegetative and sexual populations may have different dispersal characteristics, such as dispersal range (Werth *et al.*, 2006b) and number of diaspores released (Fig. 3b). *L. pulmonaria* has been suggested to be a heterothallic species (Zoller *et al.*, 1999). Gene flow among populations may facilitate a hitherto asexual population to become sexual in heterothallic species. Large populations produce abundant diaspores and thus maintain a high recolonisation potential. Maintaining high levels of genetic diversity within populations may therefore promote sexual reproduction as well as the potential for long-distance dispersal.

#### 4. Implications for lichen conservation

In the past, major efforts in lichen conservation have focused either on habitat conservation or species protection – that is, either “freezing” the habitat in the present state, or prolonging the life of a few survivors of a population. Our population studies emphasise the importance of the “three guiding principles of conservation biology” in their application to lichen conservation, i.e. allowing for evolutionary change, dynamic ecology and human presence (Groom *et al.*, 2006).

High conservation priority may be given to populations of extremely rare species or to populations of species for which the country has a high international responsibility, e.g. in the case of endemic lichen species. In order to effectively conserve lichen communities and populations in dynamic landscapes, in both cases the general aim is to maintain viable metapopulations linked through dispersal. Especially in epiphytic species patch-tracking metapopulations (Snäll *et al.*, 2005) face relatively frequent extinctions that require high recolonisation rates in order to maintain a constant population size over time. To achieve this, three major points need to be taken care of. First, extant large populations of rare and important lichen species need to receive strict protection. These are the propagule pools, which are essential for long-term persistence of the species. Second, at short distances (i.e., within hundreds of metres) from such propagule sources, suitable areas need to be reserved for conservation. These will become the habitats in the decades to come. The aim is to maintain a large quantity of habitat (e.g. old trees of a preferred tree species, or open soil patches for terricolous species) within the landscape at any time – also in the future. It is likely that management support is needed to develop habitat, e.g. in situations where forest succession is altered by non-native herbivores that may disturb forest regeneration. Third, in many cases viable lichen populations may only be retained if harvest of forest resources is stopped or reduced considerably. Depending on the favourable forest structure and tree species composition, this may still involve substantial management input from forest service, e.g. to favour specific tree species such as white oaks in Central Europe (Weber, 2000).

Conservation practice will notoriously be faced with conflicts and compromises and in many instances less than the optimal size of habitat will receive protected status. In such instances or when catastrophic disturbances have

drastically reduced a lichen population, direct measures to protect and augment existing populations have to reduce their risk of a future extirpation. In some cases, for species of a special concern, augmentation measures to increase local population sizes may be justified (Scheidegger *et al.*, 1998), but in general, protection of habitats and propagule pools is much preferable to costly and time-consuming population augmentations.

Successful strategies of lichen conservation will generally combine efforts to protect habitats and to maintain or improve the size, demographic and genetic structure of populations. “Artificially” rare species that were once widespread or abundant but have been reduced to small population size through human activities seem more likely to go extinct (Groom *et al.*, 2006) than species that are evolutionarily adapted to rarity (Kunin and Gaston, 1997).

The primary focus in lichen conservation should be on the maintenance of habitat quality, connectivity and size. Also in the future, land-use change involving habitat loss and degradation will likely be the single most important cause of population decline of lichens. Conservation of permanent habitats such as mountain ridges can best follow a static protection and is relatively easy to achieve compared to the conservation of dynamic habitats such as forests, grasslands, and gravel fields. Habitats, forest stands, or even entire landscapes do not need to be frozen in a traditional status (rarely practiced today) but the lichen populations need to retain a viable effective population size, and moreover, functional connectivity needs to be achieved among populations.

As with other organisms that are integrated in an ecological network, lichen conservation biology will only be successful if the species is seen as part of a community that is the result of complex interactions between climatic conditions, environmental quality and anthropogenic management.

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