The Lichenologist **45**(2): 265–276 (2013) © British Lichen Society, 2013
doi:10.1017/S0024282912000746

Transient populations in the British conservation priority lichen, *Cladonia botrytes*

Rebecca YAHR, Brian J. COPPINS and Alexandra M. COPPINS

Abstract: In the face of changing environments, conservation is tending towards an adaptive framework which accounts for the movement of species in the landscape. This makes it necessary to quantify population dynamics of species of concern. We studied the nationally scarce *Cladonia botrytes*, a priority Biodiversity Action Plan species in Britain, examining population dynamics at two scales: first, we studied the demography for two populations over a period of 13 years. The monitored populations declined to complete absence, starting from 77 mats on 19 stumps. Individual mats persisted maximally for up to 7 years, but over 78% of more than 290 individual cases persisted only 1 year, and more than 93% of mats disappeared within 3 years. Secondly, we performed a targeted regional survey of more than 800 stumps across an additional 27 sites in the centre of the lichen's distribution in Britain in 2006. The largest populations known from 1998 were revisited and found to no longer support the species; only 9 stumps in 5 sites supported *C. botrytes* in 2006. We show that *C. botrytes* in Britain is characterized by short individual and population persistence times, probably locally dependent upon vegetative succession including overgrowth and shading, and the degree of stump decay. The species' transient nature poses a particular challenge to conservation, though we identify comparable systems from which lessons may be learned.

Key words: demography, management, population dynamics, short-lived

Accepted for publication 26 *September* 2012

Introduction

Conservation of many species is challenged by the lack of specific information about critical life-stages including dispersal and establishment (Schemske *et al.* 1994); these challenges become even more acute in the face of fragmented habitats and changing climate (Heller & Zavaleta 2009; Ellis 2011), and especially for groups of organisms with few demographic studies (Ellis & Yahr 2010). Lichens are generally held up as examples of long-lived, slow-growing organisms, though ephemeral lichen species do exist (Poelt & Vězda 1990), in which life spans can be as short as a few months. Such species appear to have life cycles dictated in part by disturbance required for the creation of their habitats, for example on soils in forestry settings (Kantvilas 2005), or on small pebbles, detritus or other unstable habitats, where fast pre-emption of resources (i.e. space) is critical for reproduction (Grime 1977).

Cladonia is a genus of more than 450 species, perhaps best known for long ecological persistence in the extensive mats of *Cladonia* subgenus *Cladina* (reindeer lichens), relatively late-successional species dominating huge areas of the taiga over periods spanning many decades (Ahti 1961). In contrast, many *Cladonia* subgenus *Cladonia* are largely early-colonizing species, limited in both physical and temporal habitat availability. The circumboreal species *C. botrytes* falls into this latter group, being confined to decaying wood and bark during a relatively narrow window between appearance of the substratum and its progression through medium to advanced states of decay. It is a diminutive *Cladonia* species, often dwarfed by the other co-occurring species (e.g. larger statured lichens,

R. Yahr and B. J. Coppins: Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, UK. Email: r.yahr@rbge.ac.uk
A. M. Coppins: 37 High Street, East Linton, East Lothian, EH40 3AA.

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

mosses or vascular plants) and with local population persistence determined in part by habitat patch dynamics as stumps decay and are overtopped by bryophytes (Caruso *et al.* 2010). *Cladonia botrytes* is listed as a conservation target in several central European countries (Austria, Germany, Poland and Switzerland; Coppins & Coppins 1998) and Britain and Ireland, although it is common in northern parts of its range (e.g. Norway, northern North America; Lynge 1921; Thompson 1967; Dahl & Krog 1973).

In the UK, *Cladonia botrytes* is known from only 16 10-km grid squares, all in Scotland, 13 of which are from confirmed herbarium collections or from observations since the 1990s (Coppins & Coppins 1998; National Biodiversity Network 2012). Most occurrences are in the major watersheds of the Cairngorm Mountains, almost exclusively on cut stumps of conifers, mainly *Pinus sylvestris* (Coppins & Coppins 1998; Street 1998). In Britain, occurrences are comprised of small, continuous mats of primary squamules producing one to several podetia occupying a discrete area on the cut surface. Outside Britain, it can be a common species on stumps (Caruso *et al.* 2008), where it is found growing in more extensive swards and occupying other types of conifer lignum in the boreal-continental region of Eurasia and North America (Litterski 1992), extending to montane regions of the temperate zone (Litterski & Ahti 2004).

We present the first demographic study of *Cladonia botrytes* in Britain. We traced the occurrence of individual mats of podetia-bearing squamules (hereafter called mats) on stumps following the discovery of Britain's largest-known recent population in 1998 at Kindrogan, a Scottish Field Study Centre. Monitoring of populations of *C. botrytes* was carried out by students attending annual Lichen Identification courses, providing a unique opportunity to collect data on population dynamics of this species. We document the rapid change in population size, a trend of steady decline and eventual local extirpation. Additionally, we suggest that the life history of this lichen in the UK is largely annual, with a relatively small proportion of mats persisting more than a single year. We use these findings to frame the likely conservation implications for this species in Britain. We also base our discussion on a comparison of regional survey data from two time points across several populations.

Methods

Detailed demographic study

A site in central Scotland, at Kindrogan Field Centre, Perthshire (56°45′N, 3°33′W), was monitored since the discovery of *C. botrytes* in 1998 until its local extirpation in 2011. The site is characterized by mixed non-native conifer plantation, clear-felled probably in the late 1970s (*c.* 1978), when the stumps were created. The site was replanted with conifer, but in two places the plantings failed, creating two open, sheltered clearings where *C. botrytes* was subsequently discovered on stumps. Each year, surveys of cut stumps in two clearings were made with the assistance of members of the annual 'Introduction to Lichens Field Course' run by BJC and AMC. Clearings were separated by *c.* 100 m of plantation, and were treated as separate populations.

In Britain, *C. botrytes* 'individuals' are comprised of a small mat of basal squamules, often surmounted by one to several podetia; these so-called 'mats' tend to occupy an area of only *c.* 1 cm^2, rather than the large swards which occur in other parts of its range. Occurrences as small, isolated mats make the demographic approach of tracking individual thalli feasible. Methodology for monitoring populations of *C. botrytes* was devised by AMC: each year in April, every stump was examined and the location of each individual mat of *C. botrytes* squamules with podetia was mapped by noting compass bearing and distance from the centre of each stump. Mats of primary squamules without podetia were not counted or tracked, and multiple discrete mats could occur on a single stump. Hereafter, the individual tracked reproductive mats will be referred to as 'mats' for simplicity. The number of podetia was also counted in each mat as an estimate of reproductive output, but individual apothecia were not counted (more than one apothecium may occur on a podetium). Identification of *C. botrytes* in the field was checked in each instance by BJC, and a photographic record made.

To estimate the error in recording mat position, a known point was measured using an equivalent method by a sample of recorders, and an observed discrepancy in bearing and distance was used to combine readings that were likely to be the result of erroneous records. Sketch maps were drawn of cut stumps, including *C. botrytes* mats, stump centres, and other conspicuous 'landmarks' (e.g. stump topography, other species, bark, decay) to ensure that position data from observers were correct and unambiguous. All field data were checked by AMC, and all reliable data from hand-written records were collated by BJC and RY. Data from each clearing were treated as separate populations.

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

Population trends

A population is defined as all the individual reproductive mats occurring within a spatially-delimited area. In the demographic study, each population occupies a group of spatially clustered stumps within a small clearing. Trends in population size over time were quantified using three measures: 1) the number of stumps with extant *C. botrytes* for each clearing; 2) the total number of mats per clearing, tracked on a per-stump basis; 3) the total number of podetia within a clearing.

Where a stump was not re-found in a given year (missing data), we assumed that mats persisted in the same state as the previous year, for example assumed present in 2001 if present in 2000, though lacking data for 2001. Since individual mats could be tracked across years, persistence of mats was examined by plotting the number of years a mat was found at the same location (i.e. distance and bearing). If mats were found in the same position as a previously identified mat, it was considered the same 'individual', even if there were gaps in the observations (i.e. observed in 1999, not observed in 2000 or 2001, observed in 2002).

Spatial factors

We examined the contribution of separate stumps to the overall population size within a clearing by ranking an individual stump according to the proportion of mats which it supported during the life-span of the entire population. Spatial aggregation of colonized stumps was calculated using Geary's C statistic with a weighting factor equivalent to the proportion of mats occurring on a stump during the lifespan of the population. The expected value under a spatially random pattern is 1, with values less than 1 and approaching zero indicating positive aggregation, and values greater than 1 indicating segregation (Geary 1954). Significant clumping of colonized stumps is likely a product of frequent short dispersal events, whereas random or segregated distributions suggest a higher level of background dispersal.

Site surveys

For the wider regional surveys, field visits were carried out in September–November 2006 by searching sites previously identified (Street 1998) and newly targeted ones (Table 1). As in the demographic study, a population is defined as all the individual reproductive mats occupying a spatially-discrete site. All sites searched occupy discrete blocks of forestry or spatially-discrete areas of pine woodland. Contacts with land managers helped to identify new potential sites with conifer (mostly *Pinus sylvestris*) stumps of suitable age. Stumps were mostly between 4 and 25 years since felling, cut at about 30–70 cm from the ground. Typically, in any site, all the visible conifer stumps were searched with the assistance of a hand lens, and pine stumps were particularly targeted. For stumps where *C. botrytes* was present, the stump was measured and a species list of the cut surface assembled. Stumps without *C. botrytes* were typically not measured, as this would have proved too time-consuming. Other conifer lignum substrata were also searched wherever they were encountered within study sites. The decay state of stumps was assessed using a scoring system based on Pyle & Brown (1998) and Makinen *et al.* (2006): early stages of decay, Class I stumps have bark firmly attached with the exposed wood still hard and appearing freshly cut or only slightly bleached. Weakly decayed stumps fall into Class II, having loose bark present, outer layers of wood beginning to soften, but with the core still fairly hard, and wood able to be penetrated by a knife less than 1 cm. Medium decay or Class III is indicated by the absence of bark, a thin spongy layer in the sapwood (often indicated by blocky products of brown-rot fungi), the core of the wood still hard, but crevices indicative of sapwood sloughing beginning to form, and penetrable between 1–5 cm with a knife. Class IV stumps are often no longer circular in outline owing to breakage and decomposition.

Results

Detailed demographic study

Population trends

The populations at Kindrogan Field Centre were first discovered in 1998 and individuals were tracked for 13 years, until no further occurrences of *C. botrytes* could be found (from 2011 onwards). In the first year (1998), a single mat was recorded from a single stump; the following year, more focused exploration revealed 77 individual mats from 19 stumps distributed in two separate clearings. Of about 50–60 available stumps across the two clearings, only 25 were ever found to host *C. botrytes*. In both clearings, the general trend over the course of the study was of decline in the number of stumps colonized and in the mats and podetia recorded, but with wide fluctuations. Individual stumps were characterized by different demographic patterns (Table 2), although these were broadly similar across clearings (Fig. 1). The maximum number of mats per stump in a given year was 14, observed on Stump 18 in two separate, non-consecutive years. On average, stumps in Clearing 2 supported more mats (for stumps with mats in a given year, Clearing 1 had on average $2{\cdot}8 \pm 2{\cdot}2$ mats per stump versus $3{\cdot}9 \pm 3{\cdot}7$ for Clearing 2) and for nearly twice as many years as those in Clearing 1 (Table 2).

Our data indicate transient population dynamics of *C. botrytes*, in which a majority of mats in most years are new occurrences, with fewer examples surviving from previous

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

TABLE 1. *Sites and stumps surveyed and occurrence of* C. botrytes *by stump condition in 2006. Those representing re-surveys of known occurrences are marked in bold.*

Estate/Parcel	Site	Grid Reference*	Stumps Surveyed	Years since felling	Occupied Stumps (no. of podetia)	Decay Class and Comments
Rothiemurchus	Achnahatnich	NH925106	18	~22	1 (5)	II, III, overgrown
	Drumintoul Lodge	NH920112	40	<10	0	I, treated?
	Loch an Eilean trail	NH899077	25	>20	0	IV
Abernethy	**Clear Fell**	**NJ032156**	**25**	**?**	**0**	**burned, overgrown**
	Bognacruie	**NJ047152**	**8**	**?**	**0**	**overgrown**
	Power Lines	**NJ016156**	**15**	**?**	**0**	**overgrown**
	Duack burn	NH999166	37 *Picea*	<10	0	I
	Ryduack	NH998179	30 *Picea*	<10	0	I
Glenfeshie	Above Lodge	NN846947	25	~50	0	II & III
	Spruce stand	NN849943	50 *Picea*	<10	0	I
	Floodplain plantation	NN849943	~50 *Picea*?	<10	0	I
Curr Wood	Gate	NH995237	34	4, >20	0	I, II, III, overgrown
	Fork in Road	**NH994234**	**58**	**4, >20**	**0**	**I, II, III, overgrown**
	A95 bog	NH982227	27	>20	0	II & III
	Section D	NH989233	18	20–50?	0	IV
Ord Ban	West Lodge	NH886088	1	?	1 (4)	II & III
Kindrogan	**Clearing 1**	**NO054627**	**19**	**>20**	**0**	**II, III, IV**
	Clearing 2	NO053628	35	>20	4 (14)	II & III, IV
	Gate	NO059626	50	<10	0	II & III, overgrown
Invercauld	Keiloch	NO191908	56	<10, ~20	1 (2)	I, II & III
Alltcailleach	Powerline	NO223930	16	15–21	1 (1)	II & III
	Wood's Edge	NO223931	20	1	0	I
	Spruce stand road	NO215936	50	1	0	I
	Knockan	NO220938	25	1,15–21, >25	0	I, II, III, IV
Mar Estate	West of Lui	NO057912	35	3–9	0	I
	Derry Lodge Plantation	NO049934	35	<10	0	burned
Linn of Dee	Along road	NO064896	50	<10, >15?	0	I, II & III

* British National Grid references (map datum from Ordnance Survey of Great Britain) are given for each stump with *C. botrytes*, if found, or for the approximate centre of the site surveyed.

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

TABLE 2. *Kindrogan: mat summaries by clearing, stump and year.*

		1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Total Mats	Yrs with mats
Clearing 1	Stump															
	2	1	0	0	3	0	0	0	0	0	0	0	0	0	4	4
	3	4	4	?	3	8	0	0	0	0	0	0	0	0	20	4
	4	1	0	0	2	2	2	1	0	0	0	0	0	0	8	7
	5	1	1	0	0	1	0	1	0	0	0	0	0	0	4	7
	6	8	1	8	9	4	2	0	0	0	0	0	0	0	32	6
	7	2	2	4	0	4	0	0	0	0	0	0	0	0	12	5
	8	3	0	0	0	0	0	0	0	0	0	0	0	0	3	1
	9	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	19	–	–	–	–	2	0	0	0	0	0	0	0	0	2	1
	20	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	22	–	–	3	1	0	0	0	0	0	0	0	0	0	4	2
	25	–	–	–	–	–	–	–	–	1	2	1	5	0	9	4
	Total Mats	22	8	15	18	21	4	2	0	1	2	1	5	0	99	Avg 3·68
	Stumps Inhabited	9	4	3	6	6	2	2	0	1	1	1	1	0		
Clearing 2	Stump															
	10	1	1	0	0	0	0	0	0	0	0	0	0	0	2	2
	11	12	0	?	5	10	3	1	0	1	1	1	1	0	35	9
	12	12	3	?	7	9	10	3	2	1	1	0	0	0	48	9
	13	6	2	6	2	2	2	1	6	7	7	0	0	0	41	10
	14	7	?	4	1	7	5	4	4	4	2	0	0	0	38	10
	15	1	0	1	1	1	1	1	0	0	0	0	0	0	6	7
	16	1	0	0	1	0	0	0	0	0	0	0	0	0	2	4
	17	1	0	0	0	1	1	0	0	2	0	0	0	0	5	9
	18	14	8	12	5	14	11	9	1	9	7	2	0	0	92	11
	21	–	1	?	1	1	2	1	0	1	0	0	0	0	7	8
	23	–	–	3	2	2	2	0	0	0	0	0	0	0	9	4
	24	–	–	–	–	–	–	–	1	0	0	0	0	0	1	1
	26	–	–	–	–	–	–	–	–	1	0	0	0	0	1	1
	Total Mats	55	15	26	25	47	37	20	14	26	18	3	1	0	287	Avg 6·85
	Stumps Inhabited	9	5	5	9	9	9	7	5	8	5	2	1			
Total Mats		77	23	41	43	68	41	22	14	27	20	4	6	0	386	
Stump Total		19	9	8	15	15	11	9	5	9	6	3	2	0		

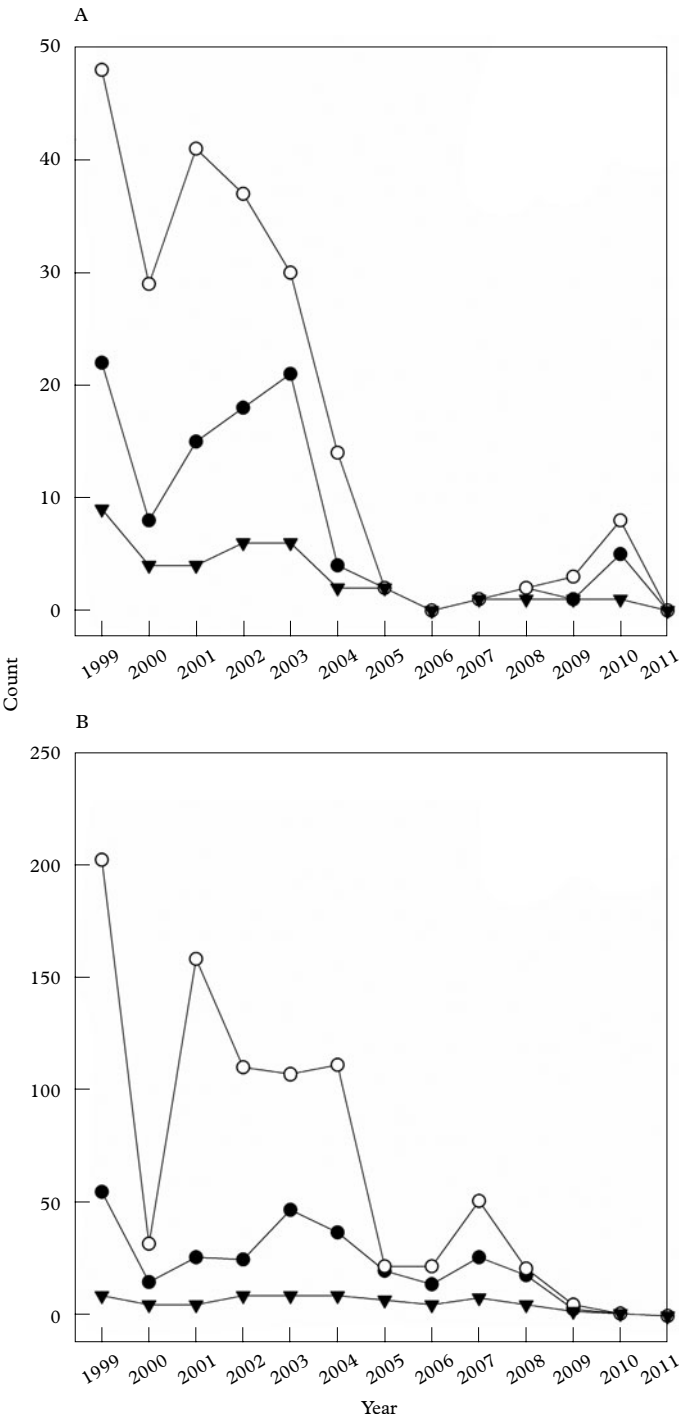


FIG. 1. Population trends of *C. botrytes* at Kindrogan Hill, Perthshire; A, Clearing 1; B, Clearing 2 (note the difference in vertical axis scaling. ▼, number of stumps colonized; ●, number of reproductive mats over all stumps; ○ total number of podetia per year.

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

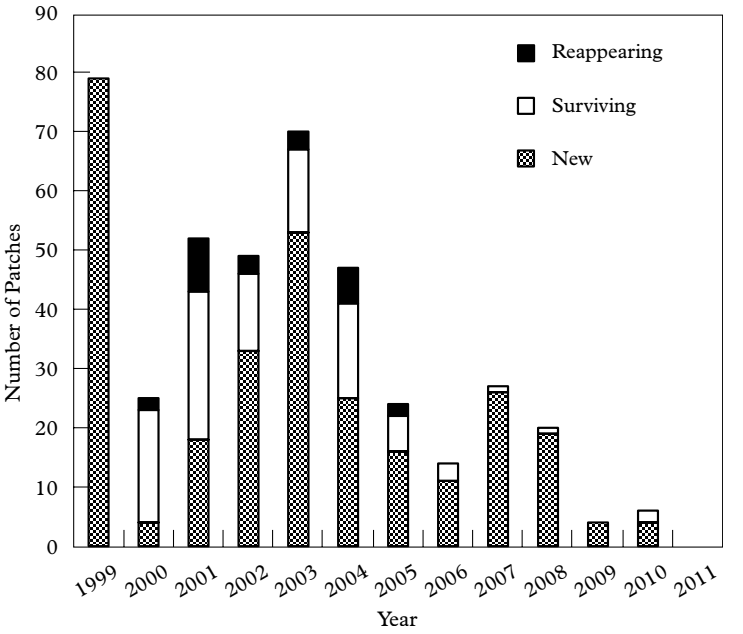


FIG. 2. Status of reproductive mats by year for all mats across clearings. Re-appearing mats are those which occupy the same position following one or more years of absence.

years, or reappearing at the same location after a period of absence (Fig. 2). First, we deal with survival of new mats: of a total of 291 unique mats with podetia ('reproductive mats') 78·7% persisted for a single year, with only 13·7% of mats persisting for 3 or more consecutive years (Fig. 3).

Secondly, we consider reappearing mats: for stumps which had been consistently recorded, there were sometimes gaps between observations of the same mat ($n = 26$), that is a mat observed at a given position in one year, was absent for one or more following years, and then subsequently reappeared in the same position. This may reflect transient dynamics of the mat, and/or the ephemeral nature of podetia used to locate the mat (i.e. squamules may have persisted, but podetia did not). If the duration of second (and in only two cases subsequent) appearances are added to those of the first, the maximal persistence of an individual reproductive mat is 7 years (2 cases, with gaps of 2 and 4 years, respectively). Six cases apparently persisted for 6 years (3 with 2-year gaps, 2 with 1-year gaps and 1 with two gaps of 1 and 2 years, respectively) (Fig. 3). Observations across years directly support the ephemeral nature of podetia. Repeat observations for mats demonstrated that individual podetia can persist over the course of two years, though podetia at an identical position to the previous year often appeared senescent in the second year.

Spatial factors

Relatively few stumps in each clearing contributed to the overall population trend, with only three stumps in each clearing accounting for more than 60% of all mats observed in that clearing across all years (Fig. 4). Based on their contribution to the populations within each clearing, occupied stumps were not spatially aggregated in either clearing (Clearing 1, Geary's $C = 0{\cdot}784$, $P > 0{\cdot}1$; Clearing 2, Geary's $C = 1{\cdot}154$, $P > 0{\cdot}1$), with the test statistic indicating a near random spatial structure in both clearings.

Regional site surveys

Across 27 sites, 685 pine stumps and 165 spruce stumps were searched in 2006. Only 8 stumps out of more than 800 searched supported *C. botrytes*, with half in a single site,

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

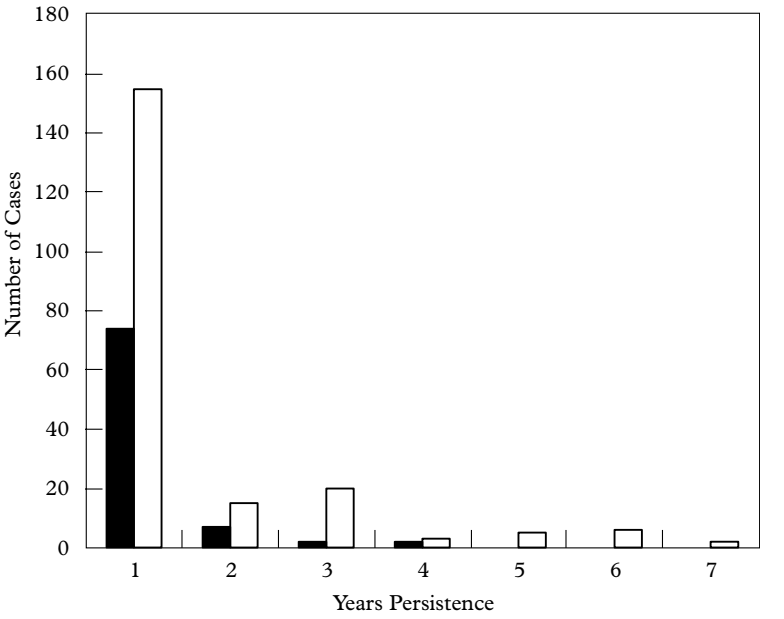


FIG. 3. Years of continuous individual mat persistence by clearing; ■ clearing 1; □ clearing 2.

Kindrogan Clearing 2 (now extirpated). In the sites where the most *C. botrytes* mats had been recorded in 1998 (e.g. Abernethy's Power Lines, Clear Fell and Bognacruie), loss of *C. botrytes* was attributed to overgrowth by shrubs, mostly *Calluna vulgaris* and *Vaccinium myrtillus*. In 2006, *C. botrytes* was found only on cut surfaces of pine, and only once on one end of a cylindrical cut piece of slash rather than a stump rooted in the ground. This slash log was upturned and mimicked a stump.

Stumps which supported *C. botrytes* in 2006 had a generally south-east facing aspect (Table 1) and belonged to decay Class II or III. The size of stumps was 57 cm in diameter on average (range 15–85), and 36 cm in height (15–80; Table 1). Stumps of less than ten years since felling did not support this species.

Discussion

We report transient population dynamics of the conservation priority species, *Cladonia botrytes*, at three spatial scales. First, at a regional scale and across the British range of the species, none of the prior populations known from 1998 was extant after eight years (2006), but five new populations were discovered, four of which were comprised of a single stump, each with a single reproductive mat (the fifth was Kindrogan Clearing 2). Secondly, we report the discovery and disappearance of two populations over the course of a 13 year demographic study at Kindrogan. Lastly, we report the transient nature of individual reproductive mats of the lichen on stumps at Kindrogan, with the vast majority (>78%) of monitored mats appearing and disappearing within one year. Local site factors appear to play an important role in population dynamics, since at the Kindrogan site Clearing 2 had more individuals with higher reproductive output and stumps which were occupied for nearly twice as long, as compared with the population in Clearing 1 (Fig. 1).

We also highlight several caveats to the interpretation of the data. The observations in our study were limited to mats of squamules with podetia. In Britain, *C. botrytes* 'individuals' are comprised of a small mat of basal squamules, often surmounted by one to several podetia (average $2{\cdot}3 \pm 2{\cdot}4$, $n = 265$ unique mats); these so-called 'mats'

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

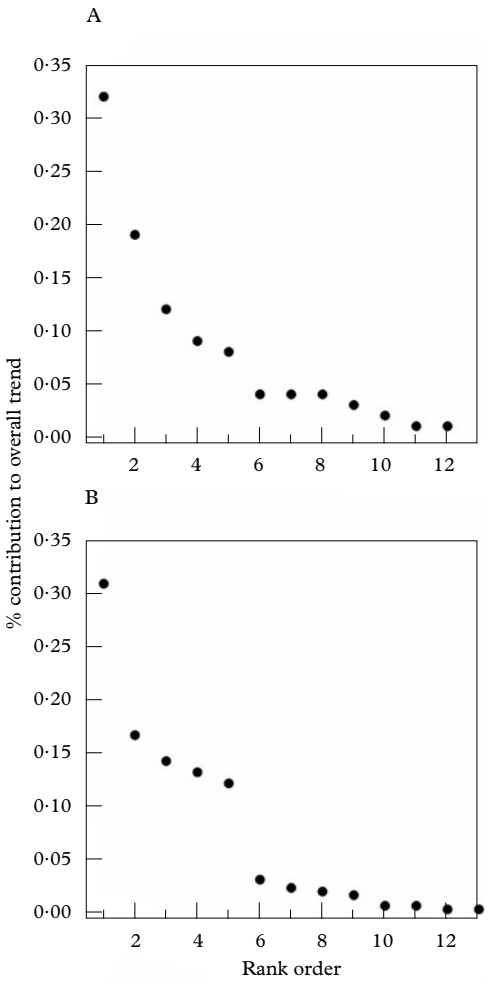


FIG. 4. Contribution of individual stumps to total population size. Ranks are given for percentage of total population across all years found on a given stump for; A, clearing 1; B, clearing 2.

tend to occupy an area of only *c.* 1 cm^2. It is possible that the mycelium or primary thallus does persist for a relatively long period in a minority of cases. However, from our data, podetia are mostly annual in persistence, and this may account for the gaps in observations for mats, if the primary thallus or mycelium persists but podetia are not always present. Furthermore, there is some ambiguity in the persistence times of reproductive mats because in a small number of cases, stumps were not relocated for a given year. In 2001, four stumps were not relocated ($n = 30$ mats), and in 2000, one stump was not relocated ($n = 7$ mats), with the assumption that mats persisted through these periods with missing data. This assumption provided a conservative estimate for persistence, which assumes mat longevity and underscores the observed transient nature of the reproductive mats. Additional factors may have had a bearing on the observed presence of podetia; for example, clearings were subject to occasional disturbance by the activities of school groups based at Kindrogan, and evidence that stump edges were sometimes scraped away by badgers foraging for invertebrates was also observed.

Given some circumspection around the persistence of mycelia or non-reproductive mats, two elements, dispersal and habitat quality, help to explain transient dynamics in *C. botrytes*.

Dispersal

All stumps within the two clearings at Kindrogan were of an equivalent age and occurred within a similar stand-setting, and there was no evidence of spatial aggregation of colonized stumps in the populations monitored. Overall population patterns within each clearing show that few of the stumps accounted for a large numerical proportion of the population. This non-aggregated pattern of heavily-colonized stumps suggests that beyond the edge of an individual stump (the habitat patch), background dispersal must be important for local population dynamics or, alternatively, that all stumps within clearings are within local dispersal ranges. Taken together with regional survey data, it seems likely that background long-distance dispersal is probably responsible for a low-frequency rain of spores at population and regional scales, in line with theoretical predictions of high dispersal for species of ephemeral habitats (Travis & Dytham 1999). Our results contrast therefore with studies on *C. botrytes* in Sweden, where the colonization of stumps increased with the rising number of nearby occupied stumps (Caruso *et al.* 2010). In that study, colonization also decreased with increasing decay of stumps, showing the sensitivity of the species to habitat patch dynamics as well as demographic factors (Caruso *et al.* 2010).

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

Habitat Quality

Observations of *C. botrytes* were made on stumps only in decay classes II and III, corresponding to weak to medium decay stages, following classifications commonly in use for describing decomposition of logs (e.g. Pyle & Brown 1998; Makinen *et al.* 2006). Likewise, the populations at Kindrogan Field Centre occupied stumps from about 20–30 years since felling, slightly older than the peak abundances found in a Swedish study, where *C. botrytes* was most abundant on stumps 12–13 years since felling (where stumps normally decay about 20 years after felling; Caruso *et al.* 2008). We surmise that *C. botrytes* was likely to have been present on the Kindrogan stumps for several years prior to its discovery there in 1998.

Wood decomposition is known to correlate with microenvironmental factors such as moisture content, though autogenic factors (especially competition) may be equally important in determining the occurrence of the diminutive *C. botrytes*. For this species, a narrow temporal window may exist between felling of pines and overgrowth of the understorey and other larger-statured and more competitive lichens and bryophytes (e.g. Caruso & Rudolphi 2009). A typical succession of lichen species on stumps may progress from normally epiphytic species to the species-rich swards on intermediate-aged substrata, and finally to those which are more commonly found on soil in later stages of decay (Krueger & Daniels 1998). These vegetation processes extend beyond the stump surface and include dynamics within the surrounding vegetation; for example, Kindrogan Clearing 1 is smaller in area than Clearing 2, with stumps more subject to shading and needle deposition from surrounding conifers. This difference may account for shorter overall persistence times of the population in Clearing 1, and for the loss of *C. botrytes* on the affected stumps near the clearing edges. Likewise, the sites from 1998 with the most *C. botrytes*, and from which the species was absent in 2006 surveys, had been overgrown by shrubs, mostly *Calluna vulgaris* and *Vaccinium myrtillus*. This is partly explained by changes to deer management across Scotland, with increased culling of red deer during 1994–2000 following the Deer (Scotland) Act (1996), and persistently high cull levels through to 2009 (Anon. 2001, 2006). Consequently, habitats have experienced lower grazing pressure during the 1990s and 2000s than over the last century. In Scotland, grazing is associated with a decrease in both vegetation height and biomass with increasing deer density (Baines *et al.* 1994; Hegland *et al.* 2006). The effects of deer on *Calluna vulgaris* and *Vaccinium myrtillus*, that is decreasing cover and height (Baines *et al.* 1994), suggest deer maintain an open understorey, conditions associated with the occurrence of *C. botrytes* and partly explaining its decline at sites with overgrown stumps. The addition of taller stumps to the landscape is currently being implemented in some pinewoods as a way to promote habitat diversity, and this may have the added benefit of providing longer-lived habitat patches for this species and others (Coppins & Coppins 2006; Rothero 2008).

The threat status of *Cladonia botrytes* in Britain can be explained by factors which integrate its life-history with the man-made habitat in which it occurs. The species' landscape-scale rarity may be explained by infrequent long-distance dispersal, that is dispersal limitation (Sillett *et al.* 2000), and/or the limited availability of a suitable local habitat. Untangling dispersal limitation from habitat limitation requires careful study, but experimental evidence has demonstrated dispersal limitations in epiphytic lichen species of old forests (Dettki *et al.* 2000; Hilmo & Sastad 2001) and it has been shown experimentally for wood-inhabiting decay fungi (Edman *et al.* 2004). Habitat limitation is known for patch-tracking species, with the loss of a patch (e.g. overgrowth or decay of a stump) resulting in local extinction (Fedrowitz *et al.* 2012). Similar to the landscape-scale trend of over-topping, stumps for the Kindrogan populations were increasingly shaded by the extension of adjacent conifer canopy, including litter rain from larch, and were altered by decay and the overgrowth of bryophytes and other *Cladonia* spp.

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

Conclusions

In Britain, the absence of old-growth stand structure and dynamics in the core part of *C. botrytes* range means that sympathetic habitat management is likely to offer the most tangible means of ensuring viable populations. For *C. botrytes*, this includes a continuous supply of suitable habitat across the landscape within the known range of the species, including maintaining sufficient deadwood habitat in the form of stumps and slash (offcut 'waste' wood from forestry operations) in early to middle stages of decay, with sufficient grazing pressure to prevent overgrowth by ground-layer vegetation. Provision of small, open clearings within forestry plantations, where stumps are sheltered but well-lit and deer are available to graze developing shrub layers to prevent stumps becoming overshaded, is recommended. Such targeted habitats will benefit other forms of wildlife which favour sheltered but well-lit glades within forest habitats (e.g. Fuller *et al.* 2007). A management goal within *C. botrytes*' British range is to increase the biodiversity of pinewoods by promoting deadwood habitats and their specialist species (e.g. Humphrey *et al.* 2002a, b; Rothero 2008). Recommendations for introducing new stumps above the height of the understorey will likely accommodate *C. botrytes* by providing cut-pine surfaces that will remain a suitable habitat long enough to be both suitably decayed but not overgrown by faster-growing vascular plants. The conservation of this diminutive and dynamic species must be thought of at the landscape scale, as local extinctions appear frequent, and a regional integrated approach to provide suitable habitat in a periodic way must be considered.

In contrast to the common perception of lichens as being long-lived organisms, we conclude that *C. botrytes* and probably other lichen species are transient and rare and encompass a unique set of conservation challenges. Analogues for this dynamic system are 'hyperdispersed and ephemeral' epiphytic orchids (Tremblay *et al*. 2006) or saproxylic insects with 'boom and bust' population dynamics (e.g. Lemperiere & Marage 2010).

The project was funded by the Royal Botanic Garden Edinburgh, and grants from the Royal Society for the Protection of Birds and Cairngorms National Park. Scottish Natural Heritage funded preliminary work for *Cladonia botrytes* as a Scottish Priority lichen. Chris Ellis provided valuable discussions and comments on the manuscript. Surveys were greatly assisted by the help of the following: Abernethy, Andy Amphlett; Glen Feshie, Thomas Macdonnell; Rothiemurchus, Stuart Blackhall; Curr Wood, Ern Emmett and Henry Becker; Kindrogan, and Martyn Jamieson. In addition, Colin Leslie assisted by providing maps, and both he and Jim Gillies provided helpful discussions about forest management at Glen More and Inshriach. John Spittle from Forest Enterprise provided useful site history for the clearings at Kindrogan. We acknowledge the willing and enthusiastic involvement of the students who participated in the monitoring project at Kindrogan over 13 years, and especially Fraser McBirnie of Forest Research, who subsequently discovered *C. botrytes* at a new site in Curr Wood, and later refound it at Braemar. Jane Sears assisted with financial details. We are grateful for the funding, advice and assistance from these institutions and individuals.

References

Ahti, T. (1961) Taxonomic studies on reindeer lichens (*Cladonia*, Subgenus *Cladina*). *Annales Botanici Societas Zoologicae Botanicae Fennicae Vanamo* **32:** 1–160.

Anon. (2001) Deer Commission Scotland (2001) Annual Report 2000–2001. Scottish Parliament.

Anon. (2006) Deer Commission Scotland (2006) Annual Report 2005–2006. Scottish Parliament.

Baines, D., Sage, R. B. & Baines, M. M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology* **31:** 776–783.

Caruso, A. & Rudolphi, J. (2009) Influence of substrate age and quality on species diversity of lichens and bryophytes on stumps. *Bryologist* **112:** 520–531.

Caruso, A., Rudolphi, J. & Thor, G. (2008) Lichen species diversity and substrate amounts in young planted boreal forests: a comparison between slash and stumps of *Picea abies*. *Biological Conservation* **141:** 47–55.

Caruso, A., Thor, G. & Snall, T. (2010) Colonization-extinction dynamics of epixylic lichens along a decay gradient in a dynamic landscape. *Oikos* **119:** 1947–1953.

Coppins, A. M. & Coppins, B. J. (1998) *Cladonia botrytes* Species Dossier. Report for Scottish Natural Heritage and the Royal Botanic Garden Edinburgh.

Coppins, B. J. & Coppins, A. M. (2006) The lichens of the Scottish native pinewoods. *Forestry* **79:** 249–259.

Dahl, E. & Krog, H. (1973) *Macrolichens of Denmark, Finland, Norway and Sweden*. Oslo, Bergen, Tromso: Universitatesflorlaget.

Dettki, H., Klintberg, P. & Esseen, P. A. (2000) Are epiphytic lichens in young forests limited by local dispersal? *Ecoscience* **7:** 317–325.

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press

Edman, M., Kruys, N. & Jonsson, B. G. (2004) Local dispersal sources strongly affect colonization patterns of wood-decaying fungi on spruce logs. *Ecological Applications* **14:** 893–901.

Ellis, C. J. (2011) Predicting the biodiversity response to climate change: challenges and advances. *Systematics and Biodiversity* **9:** 307–317.

Ellis, C. J. & Yahr, R. (2010) An interdisciplinary review of climate change trends and uncertainties: lichen biodiversity, arctic-alpine ecosystems and habitat loss. In *Climate Change, Ecology and Systematics* (T. R. Hodkinson, M. B. Jones, S. Waldren & J. A. N. Parnell, eds): 457–489. Cambridge: Cambridge University Press.

Fedrowitz, K., Kuusinen, M. & Snall, T. (2012) Metapopulation dynamics and future persistence of epiphytic cyanolichens in a European boreal forest ecosystem. *Journal of Applied Ecology* **49:** 493–502.

Fuller, R. J., Smith, K. W., Grice, P. V., Currie, F. A. & Quine, C. P. (2007) Habitat change and woodland birds in Britain: implications for management and future research. *Ibis* **149:** 261–268.

Geary, R. C. (1954) The contiguity ratio and statistical mapping. *The Incorporated Statistician* **5:** 115–145.

Grime, J. P. (1977) Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111:** 1169–1194.

Hegland, S. J., Rydgren, K. & Seldal, T. (2006) The response of *Vaccinium myrtillus* to variations in grazing intensity in a Scandanavian pine forest on the island of Svanoy. *Canadian Journal of Botany* **83:** 1638–1644.

Heller, N. E. & Zavaleta, E. S. (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* **142:** 14–32.

Hilmo, O. & Sastad, S. M. (2001) Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. *Biological Conservation* **102:** 251–259.

Humphrey, J., Stevenson, A., Whitfield, P. & Swailas, J. (2002a) *Life in the Deadwood: A Guide to Managing Deadwood in Forestry Commission Forests*. Edinburgh: Forestry Commission.

Humphrey, J. W., Davey, S., Peace, A. J., Ferris, R. & Harding, K. (2002b) Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biological Conservation* **107:** 165–180.

Kantvilas, G. (2005) Two ephemeral species of the lichen genus *Absconditella* (*Stictidaceae*) new to Tasmania. *Muelleria* **21:** 91–95.

Krueger, O. & Daniels, F. J. A. (1998) A short account on lichen succession on cut surfaces of Scots pines. *Herzogia* **13:** 231–233.

Lemperiere, G. & Marage, D. (2010) The influence of forest management and habitat on insect communities associated with dead wood: a case study in forests of the southern French Alps. *Insect Conservation and Diversity* **3:** 236–245.

Litterski, B. (1992) Verbreitung einiger Flechtenarten in Europa. *Herzogia* **9:** 149–166.

Litterski, B. & Ahti, T. (2004) World distribution of selected European *Cladonia* species. *Symbolae Botanicae Upsalienses* **34:** 205–236.

Lynge, B. (1921) Studies on the lichen flora of Norway. *Videnskappelskapets Skrifter. I. Matematisk-Naturvidenskabelig Klasse* **7:** 1–252.

Makinen, H., Hynynen, J., Siitonen, J. & Sievaneni, R. (2006) Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. *Ecological Applications* **16:** 1865–1879.

National Biodiversity Network (2012) *Cladonia botrytes* Scottish Sites Database record data Retrieved 30 April 2012, from http://data.nbn.org.uk

Poelt, J. & Vězda, A. (1990) Über kurzlebige Flechten – On shortliving lichens. *Bibliotheca Lichenologica* **38:** 377–394.

Pyle, C. & Brown, M. M. (1998) A rapid system of decay classification for hardwood logs of the eastern deciduous forest floor. *Journal of the Torrey Botanical Society* **125:** 237–245.

Rothero, G. (2008) *Looking After Green Shield-moss (*Buxbaumia viridis*) and Other Mosses and Liverworts on Dead Wood*. Back from the Brink Management Series. Stirling: Plantlife.

Schemske, D. W., Husbands, B. C., Ruckelshaus, M. H., Goodwillie, C., Parker, I. M. & Bishop, J. G. (1994) Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75:** 584–606.

Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R. & Ruchty, A. (2000) Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* **10:** 789–799.

Street, S. (1998) Cladonia botrytes *Pilot Survey in Badenoch and Strathspey*. Edinburgh: Scottish Natural Heritage.

Thompson, J. W. (1967) *The Lichen Genus* Cladonia *in North America*. Toronto: University of Toronto Press.

Travis, J. M. J. & Dytham, C. (1999) Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London, Series B* **266:** 723–728.

Tremblay, R. L., Melendez-Ackerman, E. & Kapan, D. (2006) Do epiphytic orchids behave as metapopulations? Evidence from colonization, extinction rates and asynchronous population dynamics. *Biological Conservation* **129:** 70–81.

https://doi.org/10.1017/S0024282912000746 Published online by Cambridge University Press