Bryophyte Surveys Ltd




Population status and ecology of *Codonoblepharon forsteri* at Burnham Beeches

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INTRODUCTION

Codonoblepharon forsteri (Dicks.) Goffinet is a southern-temperate suboceanic moss (Hill and Preston 1998), limited to Europe and North Africa (Sérgio and Garcia 2019). Morphologically unusual, its phylogenetic affinities have been controversial, and historically it has been placed in the genus *Euzygodon* Jur. Based on molecular data, Goffinet et al. (2004) transferred the species from *Zygodon* Hook. & Taylor to *Codonoblepharon* Schwägr. Calabrese (2006) suggested *Codonoblepharon* should be treated at subgeneric rank within *Zygodon*, whilst Matcham and O'Shea (2005) concluded the species does not fit well in either *Codonoblepharon* or *Zygodon*. Recently, its position within *Codonoblepharon* is supported by a study of the evolutionary history of Orthotrichoideae (Draper et al. 2021). Due to its general rarity and recent declines noted in some countries, *C. forsteri* is listed as 'Endangered' on the European Red List (Hodgetts et al. 2019; Sérgio and Garcia 2019) and given limited occurrence outside Europe, there is concern it may qualify for inclusion on the world IUCN Red List.

In Britain, where *C. forsteri* is considered 'Endangered' (Callaghan and Hodgetts in prep.), it survives in three areas of southern England, at Burnham Beeches (Buckinghamshire, v.-c. 24), Epping Forest (South Essex, v.-c. 18, and North Essex, v.-c.19) and the New Forest (South Hampshire, v.-c. 11). It is long-extinct in South Somerset (v.-c. 5) and Worcestershire (v.-c. 35) (Blockeel et al. 2014), and there is concern that it is undergoing a continuing decline at all of the extant sites (Adams 2019; Rumsey 2005, 2014; Woolner 2015). In England, the moss is considered to be of principal importance for conservation under Section 41 of the Natural Environment and Rural Communities Act 2006. The aim of this study is to investigate the population status and ecology of the species at Burnham Beeches.

***Codonoblepharon forsteri*.**

METHOD

Study site

The study site comprises Burnham Beeches National Nature Reserve (NNR) (51°33'31"N, 0°37'53"W; 49–81 m a.s.l.; 220 ha), which includes mature and developing woodland on acid soils, old coppice, grassland, mires, scrub and heathland (Read 2010). The principal feature of the site is ancient deciduous woodland, originally developed in a wood pasture system that combined the grazing of domestic animals with the pollarding of trees. Pollarding was the historical practice of cutting the top off a tree at ca. 2.5 m above ground level. At the point of cutting, or below, new shoots grew. This new wood, and the associated foliage, would be harvested on a rotation of ca. 15–25 yr and was used for fuel, small scale timber and fodder (Read 1991, 2010). Many of the pollards at Burnham Beeches are now ancient, predominantly ca. 400 yr old, and comprise *Fagus sylvatica* L. (European beech) and *Quercus petraea* (Matt.) Liebl. (sessile oak) (Read et al. 1996). The climate is oceanic, with 116 raindays yr^{-1} and average temperatures of 16.6°C during the hottest month (July) and 3.6°C during the coldest month (January) for the period 1961–2002 (Met Office data supplied through the UK Climate Impact Programme). The area is managed by the City of London Corporation, and is included within Burnham Beeches Site of Special Scientific Interest (SSSI) and Burnham Beeches Special Area of Conservation (SAC).

Geographic coordinates

Geographical coordinates follow the Ordnance Survey (OS) National Grid reference system. Grid cells are referred to by the coordinates of the southwest corner. Geographic coordinates were logged in the field using a hand-held GPS unit (Garmin GPSMAP 64s, Garmin Ltd, Olathe, USA), which reported an accuracy of ca. 5 m.

Tree inventory

An existing tree inventory, maintained by the City of London Corporation, was utilised for the present study. All of the ancient pollards within the site are tagged and the inventory includes accurate geographic coordinates of their locations.

Survey of previously known host trees

An inventory of all trees that are known to have been occupied by *C. forsteri* within the study area was compiled from: (i) records within the national recording database of the British Bryological Society (BBS), held by the Biological Records Centre (Wallingford, UK); (ii) records held by the City of London Corporation; (iii) reports of previous surveys (Rumsey 2005; Sanderson 2020; Woolner 2008, 2015); and (iv) correspondence with various bryologists. During April 2020, a search was made for all trees (n = 76) within the subsequent inventory. When a tree was refound, the presence/absence of the moss on the tree was determined following a thorough search, utilising a 20x LED hand lens. When *C. forsteri* was absent from a tree, reasons for its loss were determined with reference to photographs from previous survey work (Rumsey 2005; Woolner 2008, 2015). Losses were classified as: 1 – host tree death; 2 – competitive exclusion; 3 – root hole burial by leaf litter; 4 – root hole closure by callus overgrowth; 5 – root death; 6 –excessive shade by vegetation; and 7 – indeterminate.

Survey of random sample of veteran pollards

A total of 298 veteran pollards of *F. sylvatica* was determined to be alive within the study site following a tree survey in 2018. A random sample of 20% of these trees (*n* = 59) was visited and a detailed search for *C. forsteri* undertaken.

Detailed survey of woodland compartments

Three compartments of woodland within the site were selected and a detailed search was undertaken of all trees within each compartment for *C. forsteri*.

Population size and abundance of *Codonoblepharon forsteri*

Following Bergamini et al. (2019), an 'individual-equivalent' of *C. forsteri* is considered to comprise a host tree occupied by the moss, and population size is a count of the host trees. Abundance of *C. forsteri* on an occupied tree was measured by counting the number of occupied 10 x 10 cm grid cells. If a grid cell was occupied only by protonema of *C. forsteri*, this was noted following confirmation of the identification of the protonema by microscopy.

Niche occupancy

At each tree found to be occupied by *C. forsteri*, the following variables were measured: (i) tree species; (ii) whether the tree was alive or dead; (iii) circumference of the tree trunk at 1.5 m above ground; and (iv) microhabitat type. The latter was categorised as: 1 – root knothole; 2 – seepage zone on tree trunk; and 3 – deadwood of tree trunk.

RESULTS

Survey of previously known host trees

Prior to the present survey, 76 trees within the study site are known to have been occupied by *C. forsteri*. Most of these (*n* = 73; 96%) are based on records collected since 2000. Seventy-one (93%) of the trees were refound during the present survey. Details of current and former trees occupied by *C. forsteri* are provided in Appendices 1–3. Those trees which could not be refound included A3, A7, A9, A10 and A16 (Rumsey 2005), none of which were refound by Woolner (2008, 2015). Of the 71 trees refound, *C. forsteri* was present on 33 (46%). Two main causes were responsible for the loss of *C. forsteri* from previously occupied trees, namely competitive exclusion and tree death. Burial of root holes by leaf litter has also been a frequent cause, whilst rare reasons are development of excessive shade, root hole closure due to callus overgrowth, and root death (Figure 1).

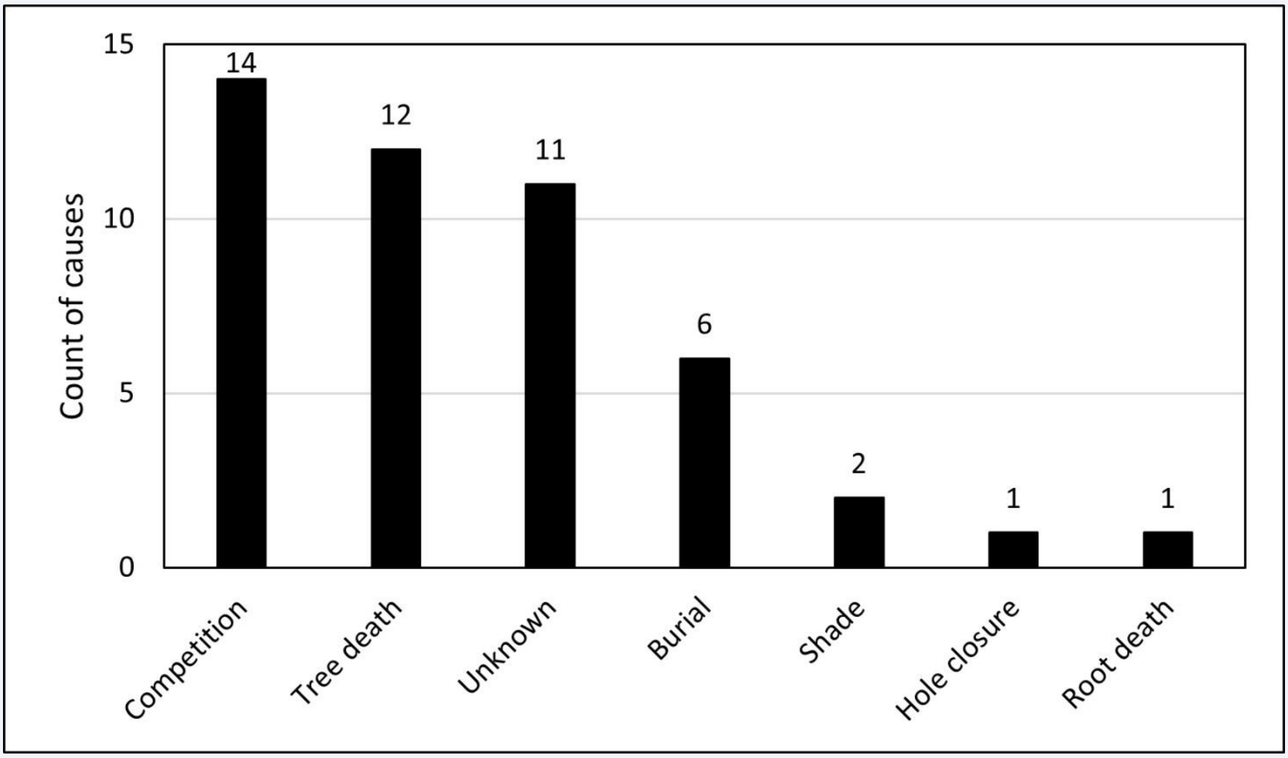

Figure 1. Causes of loss of *Codonoblepharon forsteri* from previously occupied trees at Burnham Beeches. Competition = competitive exclusion by other bryophytes or vascular plants, Tree death = death of host tree, Unknown = cause undetermined, Burial = burial of root knotholes by a build-up of leaf litter, Shade = development of excessive shade by vegetation, Hole closure = callus overgrowth of root knotholes, Root death = death of root of living tree.

Survey of random sample of veteran pollards

Of the 59 veteran pollard *F. sylvatica* included within the random sample, *C. forsteri* was present on 11 (19%). This suggests that of all the veteran pollard *F. sylvatica* that were alive in 2018 (*n* = 298), ca. 55 presently host *C. forsteri*.

Detailed survey of woodland compartments

Results from the detailed surveys of woodland compartments are shown in Table 1. The density of trees occupied by *C. forsteri* averaged 1.1 trees ha^{-1} (range = 0.56–2.1 trees ha^{-1}).

Table 1. Results of detailed surveys for *Codonoblepharon forsteri* within woodland compartments at Burnham Beeches.

Compartment	Area (ha)	N° trees occupied by *C. forsteri*	Density of trees occupied by *C. forsteri* (trees ha^{-1})
1	7.2	4	0.56
2	4.2	9	2.1
3	5.4	5	0.93
Total	16.8	18	1.1

Population size and abundance of *Codonoblepharon forsteri*

Codonoblepharon forsteri was found on 47 trees during the present survey. An accurate estimate of the total population size at Burnham Beeches is not possible based on current information. However, whilst the species is not limited to veteran pollards (see below), it is not presently known to occur within woodland compartments at Burnham Beeches that do not contain these trees. Of the 220 ha of habitat within the study site, 105 ha comprises woodland compartments which contain veteran pollards. Therefore, given an average density of 1.1 trees ha^{-1} within the woodland compartments surveyed in detail (see above), a total population of ca. 115 occupied trees at Burnham Beeches seems to be a reasonable estimate based on current information.

A total of 198 10 cm grid cells was found to be occupied by *C. forsteri* on the 47 host trees found during the present survey. Most of these grid cells (*n* = 154; 78%) contained gametophytes. Sporophytes were commonly present also, but their frequency was not recorded due to time constraints. The remainder of the grid cells occupied (*n* = 44; 22%) contained only protonema, and most of these (*n* = 33) were on a single tree. On each tree occupied, *C. forsteri* typically occurs in very small quantity, with the great majority of trees supporting ≤3 occupied 10 cm grid cells (*n* = 40; 85%). Five trees (11%) supported ≥10 occupied 10 cm grid cells and the two trees that supported ≥30 occupied grid cells are clearly exceptional (Figure 2).

Niche occupancy

Codonoblepharon forsteri was found only on *F. sylvatica* and almost exclusively (*n* = 45; 96%) on living trees. The two dead trees occupied were both recorded as alive during a tree survey in 2018, so their deaths are recent. Three main types of microhabitat are occupied within the site (Figure 3). By far the most frequent is root knotholes, inhabited on 41 trees (87%). Seepage zones on trunks were occupied on 5 trees (11%) and deadwood of trunks was occupied on 2 trees (4%). Host trees are typically large, with a trunk circumference averaging 294 cm (range = 44–570 cm; *n* = 47), though this sample is likely to be bias towards larger trees because they have attracted more attention from surveyors. Within the three woodland compartments where all trees were searched in detail (i.e. an unbiased sample), host trees of *C. forsteri* included a young tree but the remainder were mature to ancient, with medium to large trunk circumferences (Figure 4). Eight (44%) of the trees occupied within these compartments were veteran pollards.

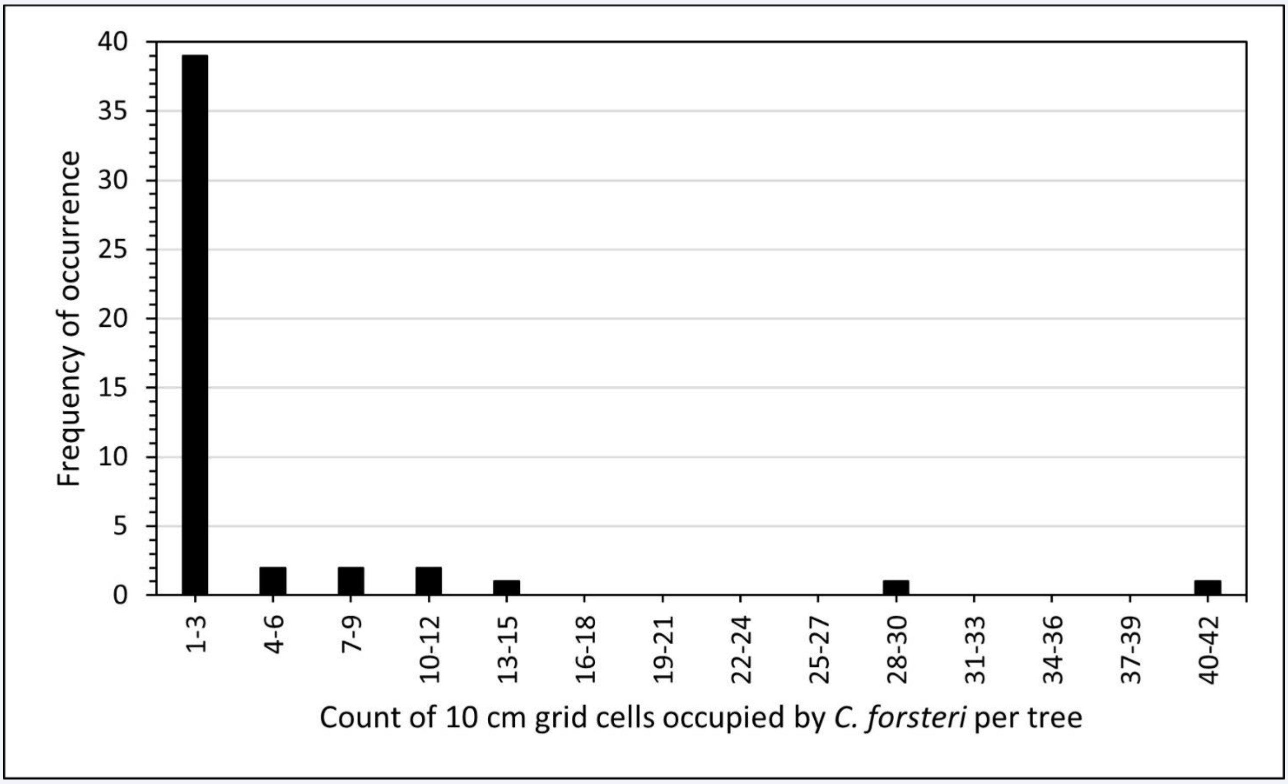

Figure 2. Frequency distribution of counts of 10 cm grid cells occupied by *Codonoblepharon forsteri* per host tree at Burnham Beeches.

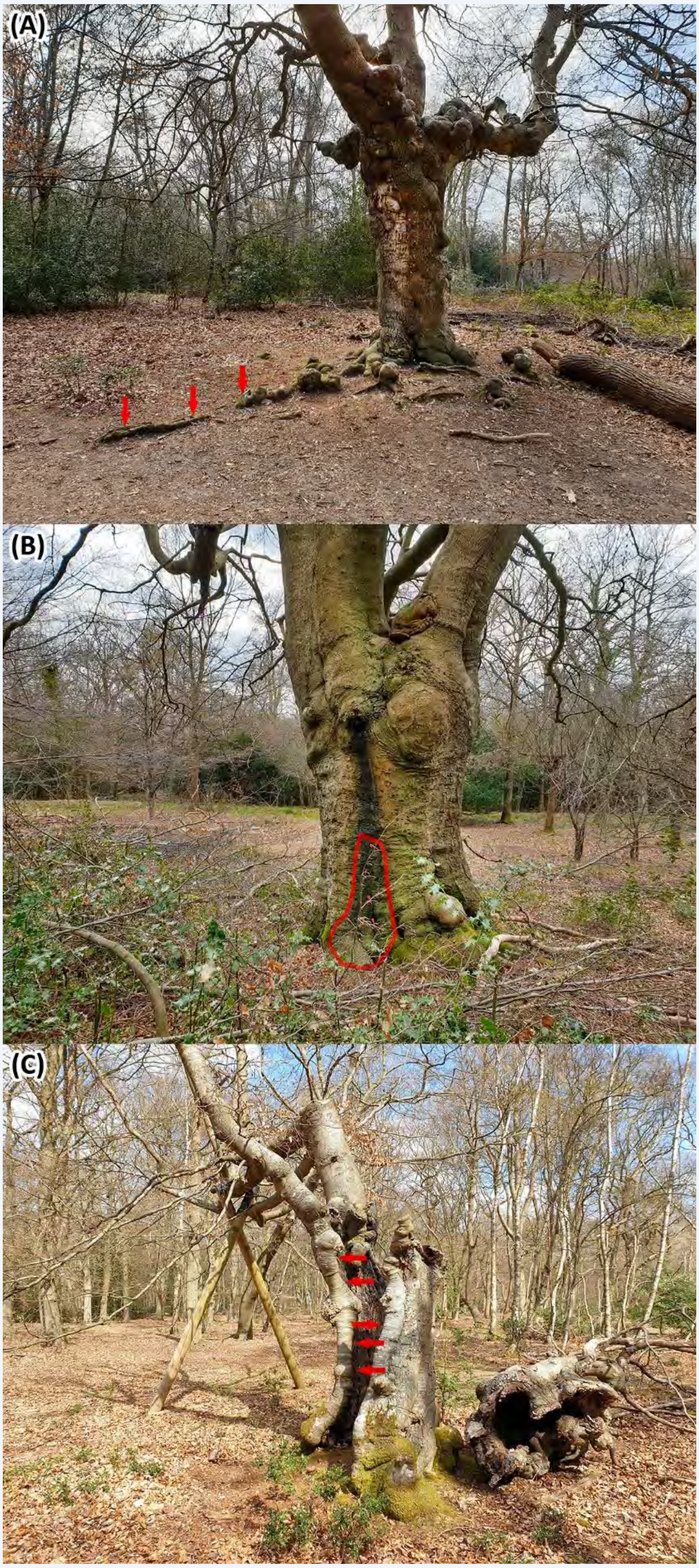

Figure 3. Microhabitat types occupied by *Codonoblepharon forsteri* at Burnham Beeches, including (A) root knotholes, (B) seepage zones on tree trunks, and (C) deadwood of tree trunks.

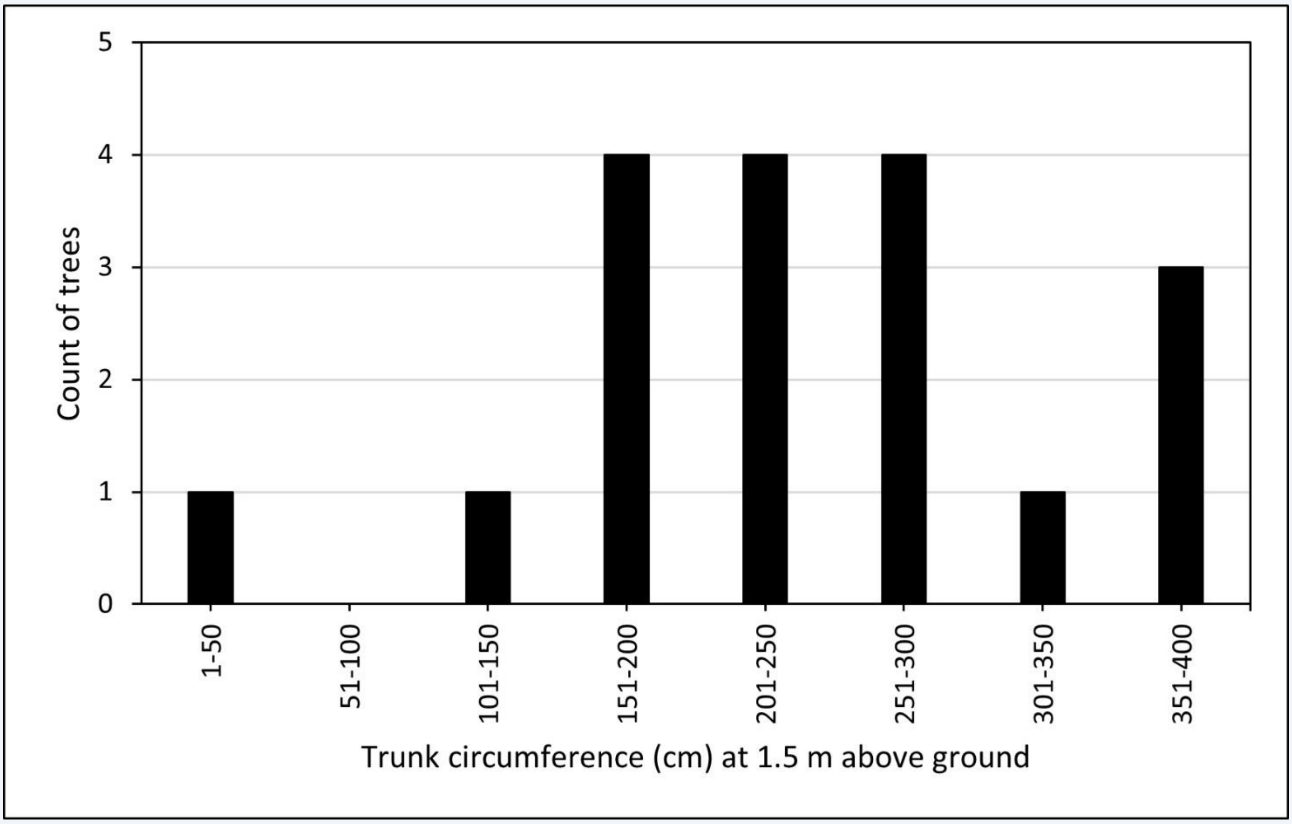

Figure 4. Frequency distribution of circumference of trunks of trees occupied by *Codonoblepharon forsteri* within three woodland compartments where all trees were surveyed at Burnham Beeches.

DISCUSSION

This study confirms the occurrence of *C. forsteri* on 47 trees at Burnham Beeches and provides data which suggests the actual total is ca. 115 trees, of which ca. 55 are ancient pollards. This appears to be broadly similar to populations in Epping Forest and the New Forest, where ca. 47 and 30 trees are presently known to be occupied, respectively (K.J. Adam pers. comm.; Callaghan 2021; Rumsey 2015). Only nine sites globally have been confirmed as supporting >10 host trees for *C. forsteri*, though detailed surveys have rarely been undertaken outside Britain (Callaghan et al. submitted). All current host trees at Burnham Beeches are *F. sylvatica*, which is also the case in Epping Forest and the New Forest (Adams 2019; Adams and Rumsey 2005; Rumsey 2014), despite seemingly suitable habitat being provided frequently by other tree species within these woodlands, including for example *Ilex aquifolium* L., *Betula pendula* Roth and *Q. petraea*. Indeed, records of its occurrence in Britain on trees other than *F. sylvatica* are limited to an *Acer campestre* L. near Harvington (Worcestershire) during 1905–1910 (Proctor 1961) and the root of a *B. pendula* at Burnham Beeches in 1966 (Little 1967). There is also a verbal account that it was once found by F. Rose on the trunk seepage of a *Q. petraea* (Tree No. 1285) at Burnham Beeches sometime in the 1970s. However, a search of the tree in 1980 by K.J. Adams failed to refind it (K.J. Adams pers. comm.), as have other subsequent searches (Rumsey 2005), suggesting the record should be treated with some uncertainty. The oak still survives, but no longer supports a trunk seepage.

Reasons for the overriding occurrence of *C. forsteri* on *F. sylvatica* in Britain are unclear and deserve further investigation. It is especially difficult to fathom when considering the moss occurs commonly on other tree species in the Mediterranean, including both broadleaved and coniferous species, such as *Abies cephalonica* Loudon, *A. pinsapo* Boiss., *Acer monspessulanum* L., *Olea europaea* L., *Quercus ilex* L., *Q. canariensis* Willd., *Q. faginea* Lam., *Q. ithaburensis* Decne., *Q. pubescens* Willd. and *Q. rotundifolia* Lam. (Aleffi 2017; Blockeel et al. 2014; Calabrese 2006; Erdağ and Kirmaci 2010; Jones 1956; Terroba et al. 2019). A possible reason for the importance of *F. sylvatica* in Britain could simply be related to the commonness of the tree and its propensity to provide potential niche space for the moss. It is a shallow-rooted tree and damage to exposed roots often results in the formation of rot-holes as a ring of callus grows around a wound, forming a key microhabitat for *C. forsteri*. In this regard, it is notable that exposed roots of *F. sylvatica* often suffer damage from herbivores that consume phloem tissue, especially *Sciurus carolinensis* Gmelin (American grey squirrel) (Mountford 2006; Rayden and Savill 2004), a non-native invasive species that is common in British woodlands. Indeed, fresh teeth marks that indicate *S. carolinensis* and/or *Oryctolagus cuniculus* Linnaeus (European rabbit) are commonly seen at root knot-holes of *F. sylvatica* at Burnham Beeches. Another major factor that has increased the propensity of *F. sylvatica* to provide suitable microhabitats for *C. forsteri* is the traditional practice of pollarding, which used to be a chief management measure used on this tree in England

(Rackham 1986), resulting in the frequent development of trunk holes (Read 2007) and associated dendrotelmata and trunk seepages.

Codonoblepharon forsteri is almost entirely limited to areas around water-filled rot holes ('dendrotelmata') on live trees at Burnham Beeches, most frequently root knotholes but also seepages on trunks that arise from trunk holes. Throughout its range, the moss is known to be a specialist of dendrotelmata (Callaghan et al. submitted), a niche that is rare within woodlands. Mature to ancient trees, and especially pollards, are much more likely than young trees to provide such niche space, which explains their particular importance for *C. forsteri*, as shown by the present study. Very few bryophytes are specialists of dendrotelmata, the only other in Europe being *Anacamptodon splachnoides* (Froel. ex Brid.) Brid. (Németh and Erzberger 2015; Sandron and Hugonnot 2012; Schröck et al. 2019). Why *C. forsteri* has become limited to this niche is unknown, though reasons are likely related to water-availability and perhaps also chemistry, since for example water from dendrotelmata characteristically has high concentrations of carbonate hardness, nitrate, ammonium and phosphate (Schmidl et al. 2008), all factors that could be important to the survival and growth of *C. forsteri*.

Results of this study show *C. forsteri* occurs at low density at Burnham Beeches, occupying an average of 1.1 trees ha^{-1} in suitable woodland habitat. Comparable density data are not available from other sites, though the species is commonly found on only a low portion of trees within occupied woodlands (Callaghan et al. submitted). For example, at a site considered to be particularly important for *C. forsteri* in Andalusia (Spain), Terroba et al. (2019) surveyed 1620 trees and found 62 (3.8%) were occupied by the moss, while Little (1967) searched ca. 150 trees at Burnham Beeches and found ca. 6 (4%) occupied. This is clearly related to the scarcity of dendrotelmata within most woodlands and helps to explain why a species with a relatively large geographic range is limited to a relatively small overall population (Callaghan et al. submitted).

Competitive exclusion is a key factor responsible for the loss of *C. forsteri* from previously occupied trees at Burnham Beeches, most often caused by over-growth by pleurocarpous mosses, especially *Isothecium myosuroides* Brid. This has also been noted to occur frequently in Epping Forest, where the main competitor is *Brachythecium rutabulum* (Hedw.) Schimp. (Adams and Rumsey 2005). Concern has been raised at Burnham Beeches and Epping Forest that the rate of competitive exclusion of *C. forsteri* has increased in recent decades because a decline in sulphur dioxide emissions and an increase in nitrogen deposition has favoured the growth of large pleurocarps (Adams and Rumsey 2005; Rumsey 2015), a matter that deserves further investigation.

Tree death is the second major cause of loss of *C. forsteri* from trees at Burnham Beeches, a problem that has also been highlighted at the other two sites presently occupied by the moss in Britain (Adams 2019; Rumsey 2014). This study shows the moss can survive for a few years on some trees following their death, but it has never been seen on long-dead trees in Britain and likely soon becomes extinct once a tree has died. About half of the occupied trees at Burnham Beeches are ancient pollards, averaging about 400 yr old. These old trees, of which <300 remain throughout the site, are at the end of their lives and it is feared that all will have died within the next 50 yr (H. Reed pers. comm.). Thus, over the next few decades there will be a significant decline in the population of *C. forsteri* at Burnham Beeches as the ancient pollards are lost. Encouragingly, pollarding of new *F. sylvatica* trees for conservation purposes has begun within the NNR (Read et al. 1996, 2010), of which >1300 presently occur (H. Read pers. comm.). Assuming *C. forsteri* survives the forthcoming population bottle-neck caused by the loss of the veteran pollards, which seems to be a reasonably safe assumption, these new pollards should be a major long-term benefit to the moss.

MANAGEMENT RECOMMENDATIONS

Generally, the woodland management being undertaken at Burnham Beeches appears to favour *C. forsteri*. Specific measures recommended at individual trees include the following (see Appendix 3 for tree photographs):

- Tree 1325 (SU9488184938) - Removal of beech saplings and bramble
- Tree 1440 (SU9572885726) - Removal of holly
- Tree 1551 (SU9482684850) - Removal of holly
- Tree A02 (SU9467584495) - Removal of holly
- Tree A11 (SU9504584938) - Removal of holly

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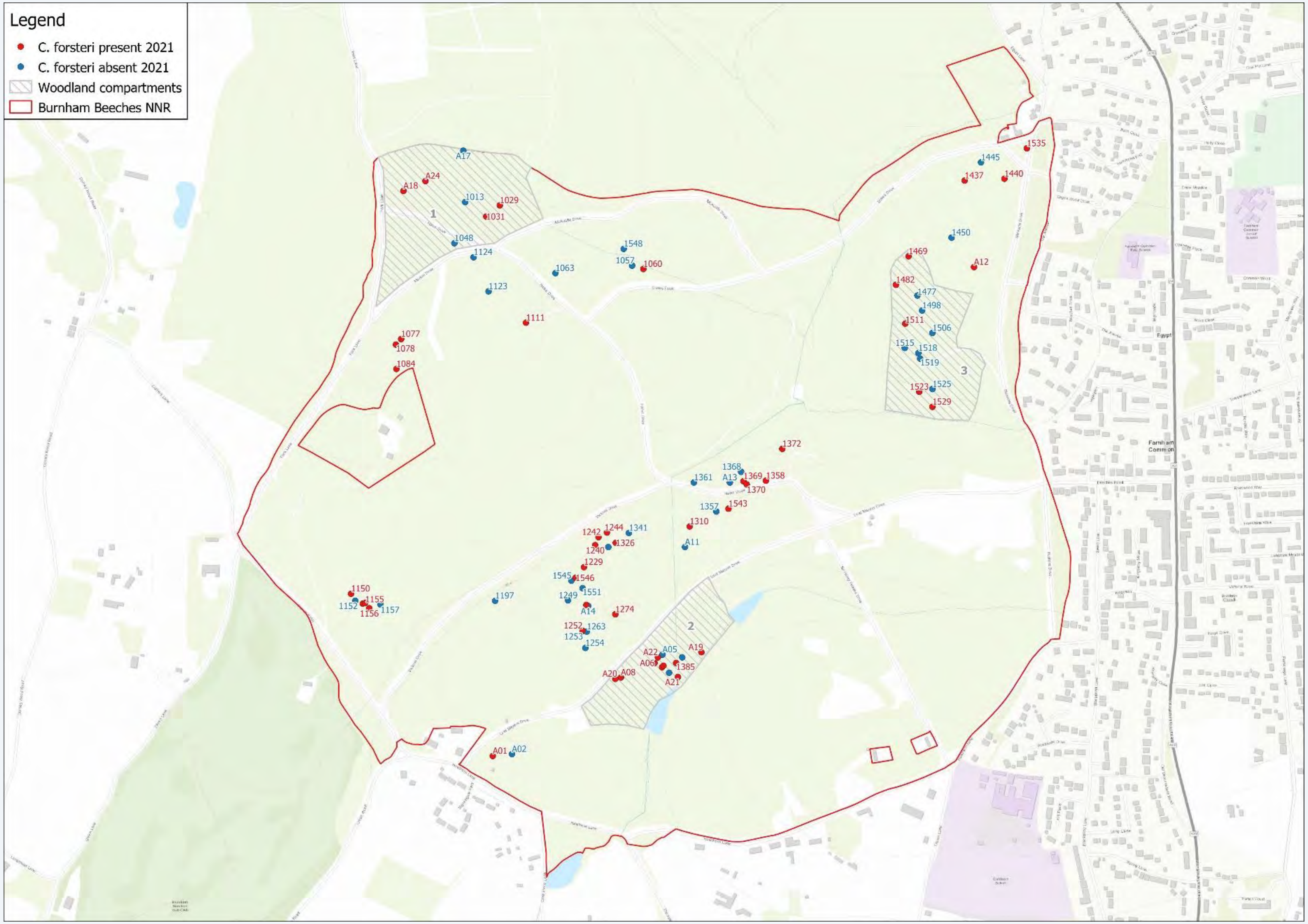
APPENDIX 1 – LOCATION OF CURRENT AND FORMER TREES OCCUPIED BY *CODONOBLEPHARON FORSTERI* AND WOODLAND COMPARTMENTS SURVEYED IN DETAIL



APPENDIX 2 – DETAILS OF CURRENT AND FORMER TREES OCCUPIED BY *CODONOBLEPHARON FORSTERI*

Tree No.	GR	Tree alive?	Girth (cm)	*C. forsteri* present in 2021?	Cause of loss[1]	Microhabitat occupied	Total 10 cm cells occupied	10 cm cells occupied by protonema only
1013	SU9457585676	No	247	No	1	Root hole	0	0
1029	SU9464985669	Yes	220	Yes	n/a	Trunk seepage	2	0
1031	SU9462085645	Yes	308	Yes	n/a	Root hole	1	0
1048	SU9455285588	Yes	401	No	2	Root hole	0	0
1057	SU9493285540	Yes	454	No	2	Root hole	0	0
1060	SU9495685533	Yes	418	Yes	n/a	Root hole	4	0
1063	SU9476885524	Yes	398	No	4	Root hole	0	0
1077	SU9443885383	Yes	332	Yes	n/a	Deadwood of tree trunk	7	0
1078	SU9442785371	Yes	301	Yes	n/a	Root hole	3	0
1084	SU9442885319	No	286	Yes	n/a	Root hole	1	0
1111	SU9470585418	Yes	372	Yes	n/a	Root hole	1	0
1123	SU9462585485	Yes	378	No	2	Root hole	0	0
1124	SU9459385558	No	?	No	1	Root hole	0	0
1150	SU9433184838	Yes	398	Yes	n/a	Root hole	1	0
1152	SU9434084823	Yes	434	No	7	Root hole	0	0
1154	SU9435684817	Yes	402	Yes	n/a	Root hole	2	0
1155	SU9436184818	Yes	320	Yes	n/a	Root hole	1	0
1156	SU9437084807	Yes	364	Yes	n/a	Root hole	2	0
1157	SU9439484815	Yes	328	No	7	?	0	0
1197	SU9463984823	No	285	No	1	Root hole	0	0
1229	SU9482984895	Yes	210	Yes	n/a	Root hole	2	0
1240	SU9485384942	Yes	249	Yes	n/a	Root hole	1	0
1242	SU9486084959	Yes	250	Yes	n/a	Trunk seepage	13	1
1244	SU9487884969	Yes	318	Yes	n/a	Root hole	2	0
1249	SU9479584824	Yes	418	No	2, 3	Root hole	0	0
1252	SU9482684759	Yes	292	Yes	n/a	Root hole	2	0
1253	SU9482784758	Yes	210	No	7	Root hole	0	0
1254	SU9483284722	Yes	347	No	2, 5	Root hole	0	0
1263	SU9483584757	Yes	227	No	7	Root hole	0	0
1274	SU9489684794	Yes	380	Yes	n/a	Root hole	2	0
1310	SU9505584982	Yes	264	Yes	n/a	Root hole	3	0
1325	SU9488184938	Yes	360	No	3	Root hole	0	0
1326	SU9489784947	Yes	230	Yes	n/a	Deadwood of tree trunk	3	0
1341	SU9492584968	Yes	220	No	7	Root hole	0	0
1357	SU9511285014	Yes	452	No	7	Root hole	0	0
1358	SU9521885080	Yes	397	Yes	n/a	Root hole	2	0
1361	SU9506485076	Yes	392	No	2, 3	Root hole	0	0
1368	SU9516585099	No	320	No	1	Root hole	0	0
1369	SU9517085079	Yes	422	Yes	n/a	Root hole	1	0
1370	SU9517785072	Yes	232	Yes	n/a	Root hole	2	0
1372	SU9525385148	Yes	387	Yes	n/a	Root hole	1	0
1384	SU9503984702	No	450	No	1	Root hole	0	0

Tree No.	GR	Tree alive?	Girth (cm)	*C. forsteri* present in 2021?	Cause of loss[1]	Microhabitat occupied	Total 10 cm cells occupied	10 cm cells occupied by protonema only
1385	SU9502684690	No	370	Yes	n/a	Root hole	1	0
1386	SU9501184669	No	300	No	1	Root hole	0	0
1437	SU9564385722	Yes	245	Yes	n/a	Trunk seepage	11	10
1440	SU9572885726	Yes	423	Yes	n/a	Root hole	3	0
1445	SU9567885761	Yes	370	No	7	Root hole	0	0
1450	SU9561585600	Yes	326	No	2	Root hole	0	0
1469	SU9552385560	Yes	265	Yes	n/a	Root hole	7	0
1477	SU9554285476	No	?	No	1	?	0	0
1482	SU9549685499	Yes	293	Yes	n/a	Root hole	2	0
1498	SU9555285444	Yes	286	No	2	Root hole	0	0
1506	SU9557485396	No	400	No	1	Root hole	0	0
1511	SU9551685416	Yes	295	Yes	n/a	Root hole	3	0
1515	SU9551585364	Yes	252	No	7	Root hole	0	0
1518	SU9554485353	Yes	353	No	3	Root hole	0	0
1519	SU9554885341	Yes	319	No	2	Root hole	0	0
1523	SU9554685270	Yes	380	Yes	n/a	Root hole	1	0
1525	SU9557485276	No	?	No	1	?	0	0
1529	SU9557485238	Yes	398	Yes	n/a	Root hole	1	0
1535	SU9577685791	Yes	411	Yes	n/a	Trunk seepage	41	33
1543	SU9513885020	Yes	384	Yes	n/a	Root hole	3	0
1545	SU9480284866	No	330	No	1	Root hole	0	0
1546	SU9481184872	Yes	256	Yes	n/a	Root hole	5	0
1548	SU9491485576	No	343	No	1, 2	Root hole	0	0
1551	SU9482684850	Yes	330	No	2, 3	Root hole	0	0
A01	SU9463484491	Yes	570	Yes	n/a	Root hole	30	0
A02	SU9467584495	Yes	390	No	2, 3, 6	Root hole	0	0
A04	SU9499684681	Yes	187	Yes	n/a	Root hole	2	0
A05	SU9499784708	Yes	210	No	2	Root hole	0	0
A06	SU9498084690	Yes	180	Yes	n/a	Root hole	3	0
A08	SU9490884659	Yes	220	Yes	n/a	Root hole	3	0
A11	SU9504584938	Yes	228	No	2, 6	Root hole	0	0
A12	SU9566385537	Yes	248	Yes	n/a	Root hole, trunk seepage	10	0
A13	SU9514185076	Yes	240	No	7	Root hole	0	0
A14	SU9483884812	Yes	117	No	7	Root hole	0	0
A15	SU9483484814	Yes	130	Yes	n/a	Root hole	1	0
A17	SU9457185786	No	320	No	1	Root hole	0	0
A18	SU9444385700	Yes	160	Yes	n/a	Root hole	2	0
A19	SU9508084713	Yes	239	Yes	n/a	Root hole	1	0
A20	SU9489684656	Yes	218	Yes	n/a	Root hole	2	0
A21	SU9503084660	Yes	139	Yes	n/a	Root hole	1	0
A22	SU9498784702	Yes	157	Yes	n/a	Root hole	1	0
A23	SU9499984684	Yes	268	Yes	n/a	Root hole	3	0
A24	SU9449085721	Yes	44	Yes	n/a	Root hole	1	0

[1]1 – host tree death; 2 – competitive exclusion; 3 – root hole burial by leaf litter; 4 – root hole closure by callus overgrowth; 5 – root death; 6 –excessive shade by vegetation; 7 – unknown.

APPENDIX 3 – PHOTOGRAPHS OF CURRENT AND FORMER TREES OCCUPIED BY *CODONOBLEPHARON FORSTERI*

1013

GR: SU9457585676
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1029

GR: SU9464985669
Date: 20 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

1031

GR: SU9462085645
Date: 20 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

1048

GR: SU9455285588
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by Isothecium myosuroides.
Management needs: n/a.

1057

GR: SU9493285540
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by Brachythecium rutabulum.
Management needs: n/a.

1060

GR: SU9495685533
Date: 14 April 2021
Zygodon forsteri abundance: four occupied 10 cm grid cells.
Trend: increase.
Cause of trend: n/a.
Management needs: n/a.

1063

GR: SU9476885524
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: callus growth over root hole.
Management needs: n/a.

1077

GR: SU9443885383
Date: 15 April 2021
Zygodon forsteri abundance: seven occupied 10 cm grid cells (on deadwood inside trunk).
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1078

GR: SU9442785371
Date: 15 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1084

GR: SU9442885319
Date: 16 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cells.
Trend: new tree found in 2021.
Cause of trend: n/a.
Management needs: n/a.

1111

GR: SU9470585418
Date: 16 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cells.
Trend: new tree found in 2021.
Cause of trend: n/a.
Management needs: n/a.

1123

GR: SU9462585485
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by Hypnum cupressiforme.
Management needs: n/a.

1124

GR: SU9459385558
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1150

GR: SU9433184838
Date: 15 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1152


GR: SU9434084823
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: unclear.
Management needs: n/a.

1154

GR: SU9435684817
Date: 15 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: increase.
Cause of trend: n/a.
Management needs: n/a.

1155

GR: SU9436184818
Date: 15 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: increase.
Cause of trend: unclear.
Management needs: n/a.

1156

GR: SU9437084807
Date: 15 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: increase.
Cause of trend: unclear.
Management needs: n/a.

1157

GR: SU9439484815
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: increase.
Cause of trend: unclear.
Management needs: n/a.

1197

GR: SU9463984823
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1229

GR: SU9482984895
Date: 13 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1240

GR: SU9485384942
Date: 13 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cells.
Trend: increase.
Cause of trend: n/a.
Management needs: n/a.

1242

GR: SU9486084959
Date: 14 April 2021
Zygodon forsteri abundance: eleven occupied 10 cm grid cells, between arrows.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1244

GR: SU9487884969
Date: 14 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells, between arrows.
Trend: lost from former root holes.
Cause of trend: root death and competitive exclusion by Isothecium myosuroides.
Management needs: n/a.

1341

GR: SU9492584968
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

1249

GR: SU9479584824
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by *Kindbergia praelonga* and burial of root holes under leaf litter.
Management needs: n/a.

1252

GR: SU9482684759
Date: 20 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

1253

GR: SU9482784758
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

1254

GR: SU9483284722
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: root death and competitive exclusion by *Isothecium myosuroides*.
Management needs: n/a.

1263

GR: SU9483584757
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

1274

GR: SU9489684794
Date: 13 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1310

GR: SU9505584982
Date: 14 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1325

GR: SU9488184938
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: n/a.
Management needs: n/a.

1326

GR: SU9489784947
Date: 14 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells, between arrows.
Trend: lost from former root holes.
Cause of trend: root death and competitive exclusion by Isothecium myosuroides.
Management needs: n/a.

1357

GR: SU9511285014
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline
Cause of trend: uncertain.
Management needs: n/a.

1358

GR: SU9521885080
Date: 14 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: decline.
Cause of trend: competitive exclusion.
Management needs: n/a.

1361

GR: SU9506485076
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion and burial of root holes by leaf litter.
Management needs: n/a.

1368

GR: SU9516585099
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1369

GR: SU9517085079
Date: 16 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: increase.
Cause of trend: n/a.
Management needs: n/a.

1370

GR: SU9517785072
Date: 16 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cell.
Trend: increase.
Cause of trend: n/a.
Management needs: n/a.

1372

GR: SU9525385148
Date: 16 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: new tree found in 2021.
Cause of trend: n/a.
Management needs: n/a.

1384

GR: SU9503984702
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1385

GR: SU9502684690
Date: 13 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1386

GR: SU9501184669
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1437

GR: SU9564385722
Date: 16 April 2021
Zygodon forsteri abundance: eleven occupied 10 cm grid cells (10 of which have protonema only).
Trend: new tree found in 2021.
Cause of trend: n/a.
Management needs: n/a.

1440

GR: SU9572885726
Date: 14 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells.
Trend: increase.
Cause of trend: uncertain.
Management needs: removal of holly.

1445

GR: SU9567885761
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

1450

GR: SU9561585600
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by Isothecium myosuroides.
Management needs: n/a.

1469

GR: SU9552385560
Date: 14 April 2021
Zygodon forsteri abundance: seven occupied 10 cm grid cells.
Trend: increase.
Cause of trend: uncertain.
Management needs: n/a.

1477

GR: SU9554285476
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1482

GR: SU9549685499
Date: 21 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

1498

GR: SU9555285444
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by Hypnum andoi.
Management needs: n/a.

1506

GR: SU9557485396
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1511

GR: SU9551685416
Date: 14 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1518

GR: SU9554485353
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: burial of root holes under leaf litter.
Management needs: n/a.

1515

GR: SU9551585364
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

1519

GR: SU9554885341
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by Isothecium myosuroides.
Management needs: n/a.

1523

GR: SU9554685270
Date: 16 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: new tree found in 2021.
Cause of trend: n/a.
Management needs: n/a.

1525

GR: SU9557485276
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1529

GR: SU9557485238
Date: 14 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cells.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1535

GR: SU9577685791
Date: 14 April 2021
Zygodon forsteri abundance: 41 occupied 10 cm grid cells (33 of these with protonema only).
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

1543

GR: SU9513885020
Date: 14 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells.
Trend: increase
Cause of trend: uncertain.
Management needs: n/a.

1545

GR: SU9480284866
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

1546

GR: SU9481184872
Date: 13 April 2021
Zygodon forsteri abundance: five occupied 10 cm grid cells.
Trend: increase.
Cause of trend: uncertain.
Management needs: n/a.

1548

GR: SU9491485576
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death and competitive exclusion by Kindbergia praelonga.
Management needs: n/a.

1551

GR: SU9482684850
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by *Isothecium myosuroides* and burial of root holes under leaf litter.
Management needs: remove holly around tree base.

A1 (FJR1, Z8)

GR: SU9463484491. First image is view from west to east. Second image is view from east to west.
Date: 13 April 2021
Zygodon forsteri abundance: 30 occupied 10 cm grid cells, scattered around locations arrowed.
Trend: uncertain.
Cause of trend: uncertain.
Management needs: n/a.

A2 (FJR2, Z10)

GR: SU9467584495
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: excessive shade from holly growth, burial of root holes by litter build-up and competitive exclusion by *Isothecium myosuroides*.
Management needs: removal of holly.

A4 (FJR4, Z4)

GR: SU9499684681
Date: 13 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: increase.
Cause of trend: uncertain.
Management needs: n/a.

A5 (FJR5)

GR: SU9499784708
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by *Isothecium myosuroides*.
Management needs: n/a.

A6 (FJR6)

GR: SU9498084690
Date: 13 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells.
Trend: increase.
Cause of trend: uncertain.
Management needs: n/a.

A8 (FJR8, Z7)

GR: SU9490884659
Date: 13 April 2021
Zygodon forsteri abundance: three occupied 10 cm grid cells.
Trend: increase.
Cause of trend: uncertain.
Management needs: n/a.

A11

GR: SU9504584938
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: competitive exclusion by Isothecium myosuroides and shading by holly.
Management needs: removal of holly.

A12 (FJR11, Z12)

GR: SU9566385537
Date: 14 April 2021
Zygodon forsteri abundance: ten occupied grid cells (three of root holes and seven of forked trunk seepage).
Trend: increase.
Cause of trend: uncertain.
Management needs: n/a.

A13

GR: SU9514185076
Date: 14 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

A14 (FJR9)

GR: SU9483884812
Date: 13 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

A15 (FJR10)

GR: SU9483484814
Date: 13 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: decline.
Cause of trend: uncertain.
Management needs: n/a.

A17

GR: SU9457185786
Date: 15 April 2021
Zygodon forsteri abundance: nil.
Trend: decline.
Cause of trend: tree death.
Management needs: n/a.

A18

GR: SU9444385700
Date: 15 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: stable.
Cause of trend: n/a.
Management needs: n/a.

A19

GR: SU9508084713
Date: 19 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cells.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

A20

GR: SU9489684656
Date: 19 April 2021
Zygodon forsteri abundance: two occupied 10 cm grid cells.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

A21

GR: SU9503084660
Date: 19 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

A22

GR: SU9498784702
Date: 19 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

A23

GR: SU9499984684
Date: 19 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.

A24

GR: SU9449085721
Date: 20 April 2021
Zygodon forsteri abundance: one occupied 10 cm grid cell.
Trend: n/a.
Cause of trend: n/a.
Management needs: n/a.