



A tale of two fires: heathland bryophyte successions at Thursley Common

Silvia Pressel, Jill Kowal and Jeff Duckett have studied bryophyte recolonisation of this heathland over 15 years, finding both expected changes and surprising results.

Thursley Common National Nature Reserve in Surrey, south-east England, suffered devastating fires covering 228 hectares on 13 July 2006 and 150 hectares on 30 May 2020 which burnt roughly 68% and 45% of the heathland respectively. When searching the literature for our article on bryophyte recolonisation of heathland on Thursley Common two years after the major fire in 2006 (Duckett *et al.*, 2008) we made a surprising discovery. Apart from general statements about the rise and fall of classic post-fire taxa like *Funaria hygrometrica* (Southorn, 1976, 1977), dating back to 1925 for Surrey heathlands (Benson & Blackwell, 1926), and *Marchantia polymorpha* (Duckett & Pressel, 2009), and a listing of *Ceratodon purpureus*, *Leptobryum pyriforme*, *Poblia nutans* and *Polytrichum juniperinum* as other post-fire specialists on British heathlands (Coppins & Shimwell, 1971; Southorn, 1976;

Hobbs & Gimingham, 1987; Burch, 2009) and Canadian boreal mixed forest (Bradbury, 2006), plus data by Clement & Touffet (1990) showing that fires lead to monogeneric dominance of *Polytrichum* species, we were unable to trace a single publication chronicling the long-term sequence of the successional changes or even a full listing of the taxa involved several years after a fire. Almost equally remarkable was the lack of detailed accounts of the reproductive cycles of a range of common heathland mosses, apart from Polytrichales (Longton & Schuster, 1983), and how these might be disrupted by fires. Further lacunae are temporal accounts of bryophyte successions immediately following fires leading to communities dominated by *Funaria*, *Marchantia*, *Ceratodon* and *Polytrichum juniperinum*, apart from a single study in Tasmania (Duncan & Dalton, 1982). This paper attempts to fill in these gaps (Figs 1, 2).



△ Figure 1. Silvia and Jill discussing the meaning of life, the universe and skewed sex ratios in *Marchantia* with James Giles, the Natural England warden of Thursley NNR. Jeff Duckett

Duckett *et al.* (2008) predicted that nutrient leaching at Thursley would lead to a decline in *Marchantia* and *Funaria*, followed by abundant sporophyte production in *Ceratodon*, *Pohlia nutans* and *Polytrichum juniperinum* but much slower recolonisation by *Dicranum scoparium*, *Hypnum jutlandicum* and *Pleurozium schreberi* and the re-establishment of *Sphagna* and their associated liverworts.

▽ Figure 3. The last of *Marchantia* after the 2006 fire: dead 2008 archegoniophores amidst *Polytrichum commune* in February 2009. Jeff Duckett



△ Figure 2. Jeff surveys a burned-out boardwalk two weeks after the 2020 fire. Miriam David

Changes between 2009 and 2020

By the spring of 2009, nearly three years after the 2006 fire, the burnt areas had changed noticeably from autumn 2008 (Table 1). *Marchantia* had completely disappeared from the dry heath: the only trace of its former abundance was dead 2008 carpocephala overtopped by *Polytrichum commune* in damp hollows (Fig. 3). Compared with around 50–80% coverage in 2008, the burnt areas in spring 2009 were more or less

▽ Figure 4. A pure carpet of *Ceratodon*, May 2009. Jeff Duckett



Table 1. Bryophyte succession at Thursley 2009–2020.

| | March 2009 | | April & October 2011 | June 2013 | 2016–2019 |
|-------------------------------|---------------------------------------|---|--|--|---------------------------|
| Species | Frequency | Reproductive state | | | |
| Dry heath | | | | | |
| <i>Campylopus introflexus</i> | Large patches | Nearly mature capsules. Caducous shoots | Very extensive thin lawns | Very extensive thin lawns | Very extensive thin lawns |
| <i>C. pyriformis</i> | Small colonies in shallow depressions | Vegetative | Small colonies being overgrown with <i>Polytrichum</i> | Occasional small colonies | Occasional small colonies |
| <i>Ceratodon purpureus</i> | Very extensive lawns | Young sporophytes with fully expanded capsules beginning to change colour | Very extensive lawns | Small patches overgrown by <i>Campylopus introflexus</i> | - |
| <i>Bryum dichotomum</i> | Rare small patches | Young sporophytes | - | - | - |
| <i>Dicranella heteromalla</i> | Occasional large patches | Dehisced capsules | Scattered patches | Scattered patches | Scattered patches |
| <i>Dicranum scoparium</i> | - | - | - | - | Occasional clumps |
| <i>Funaria hygrometrica</i> | Very rare small patches | Young sporophytes | - | - | - |
| <i>Hypnum jutlandicum</i> | - | - | Small patches | Large patches | Large patches |
| <i>Leptobryum pyriforme</i> | A few small patches | Vegetative | Scattered plants | - | - |
| <i>Pleurozium schreberi</i> | - | - | - | - | Scattered plants |
| <i>Polytrichum formosum</i> | Extensive lawns | Sporophytes with fully elongated setae but no expanding capsules. Mature male inflorescences | Extensive lawns | Extensive lawns | Extensive lawns |
| <i>P. juniperinum</i> | Extensive lawns | Sporophytes with elongated setae a few capsules beginning to expand. Mature male inflorescences | Extensive lawns | Extensive lawns | Extensive lawns |
| <i>Pohlia nutans</i> | Occasional extensive lawns | Young setae | - | - | - |
| <i>Cephaloziella</i> spp. | Scattered small colonies | Vegetative, gemmiferous | Scattered small colonies | Scattered small colonies | Scattered small colonies |

100% covered by bryophytes, particularly *Ceratodon* with young sporophytes (Fig. 4) and *Polytrichum juniperinum* and *P. formosum* with inflorescences (Fig. 5, 6). Extensive patches of

Campylopus introflexus and clumps of *Pohlia nutans* (Fig. 7) were also prominent but *Funaria* had almost disappeared and was not encountered again until after the 2020 fire. Likewise, *Pohlia*

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| | March 2009 | | April & October 2011 | June 2013 | 2016-2019 |
|-------------------------------|---|--|--|--|--|
| Species | Frequency | Reproductive state | | | |
| Wet heath | | | | | |
| <i>Sphagnum compactum</i> | Scattered single stems, small and larger patches – many regenerating from previously burnt clumps | Vegetative | Burnt cushions fully recovered | Burnt cushions fully recovered | Burnt cushions fully recovered |
| <i>S. tenellum</i> | - | - | Scattered plants around <i>S. compactum</i> hummocks | Colonies with abundant sporophytes around <i>S. compactum</i> hummocks | Colonies with abundant sporophytes around <i>S. compactum</i> hummocks |
| <i>Campylopus brevipilus</i> | - | Vegetative | - | Small colonies on <i>Sphagnum compactum</i> & <i>S. tenellum</i> | Small colonies on <i>Sphagnum compactum</i> & <i>S. tenellum</i> |
| <i>Polytrichum commune</i> | Small patches especially between <i>Molinia</i> tussocks | Sporophytes with setae just emerging from perichaetial leaves. Young male inflorescences. Up to 10 cm extension growth from 2008 male inflorescences | Extensive patches on and between <i>Molinia</i> tussocks | Extensive patches on and between <i>Molinia</i> tussocks | Extensive patches on and between <i>Molinia</i> tussocks |
| <i>Calypogeia fissa</i> | - | Vegetative, gemmiferous | - | Scattered stems on sides of <i>Molinia</i> tussocks | Scattered stems on sides of <i>Molinia</i> tussocks |
| <i>Cephalozia bicuspidata</i> | - | Vegetative, gemmiferous | - | Scattered stems on sides of <i>Molinia</i> tussocks | Scattered stems on sides of <i>Molinia</i> tussocks |
| <i>Cephaloziella</i> spp. | One or two small colonies | Vegetative, gemmiferous | Scattered colonies | Scattered colonies | Scattered colonies |
| <i>Gymnocolea inflata</i> | - | Caducous perianths | - | Scattered colonies | Scattered colonies |
| <i>Marchantia polymorpha</i> | A few thalli below <i>P. commune</i> in hollows, none on open flat heath | Dead carpocephala from 2008. No gemmae or new carpocephala | - | - | - |

nutans was not seen post-2012.

In succeeding years *Campylopus introflexus* gradually replaced *Ceratodon* (Fig. 8). Small amounts of *Cephaloziella* spp. were present from 2009 onwards but *Hypnum jutlandicum*

did not appear until 2011, with *Dicranum* and *Pleurozium* not until 2016. By 2011 there was little evidence of the 2006 fire damage to the low hummocks of *Sphagnum compactum* across the wet heath, whilst *S. tenellum* was re-establishing

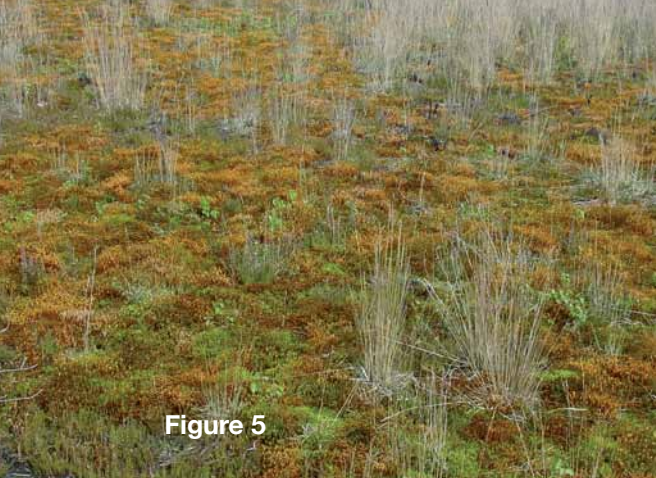


Figure 5



Figure 6



Figure 7



Figure 8



Figure 9



Figure 10



Figure 11



Figure 12



Figure 13



Figure 14

around their bases. In 2013, and thereafter, these newly established colonies produced abundant sporophytes in the early summer (Fig. 9). Burnt areas amidst these *S. tenellum* patches were the only place where we found *Campylopus brevipilus* (Fig. 10). Unlike *P. formosum* and *P. juniperinum*, *P. commune* did not become fertile until the spring of 2010 with the first sporophytes appearing in 2011. *Caylpogetia*, *Cephalozia* and *Gymnocolea* did not return to the wet heath until 2013.

The fire of May 2020

The 2020 fire, although smaller in terms of surface area, was similar in magnitude to the 2006 fire and also affected both dry (Fig. 11) and wet heath. On the latter, this fire obliterated the experimental area used to investigate competition between *Campylopus introflexus* and *C. brevipilus* (Duckett *et al.*, 2006).

◁ Figure 5. Carpet of *Polytrichum juniperinum*, May 2009.

Figure 6. Carpet of *Polytrichum formosum*, April 2017.

Figure 7. *Pohlia nutans*, abundant in May 2009.

Figure 8 *Campylopus introflexus* replacing *Ceratodon* in June 2013.

Figure 9. *Sphagnum tenellum* fruiting, June 2013.

Figure 10. *Campylopus brevipilus* growing over *Sphagnum tenellum*, June 2013.

Figure 11. Typical pre-burn dry heath vegetation, March 2019.

Figure 12. *Sphagnum compactum* and *Polytrichum commune* hummocks 56 days after the 2020 fire: new *Molinia* leaves, but no sign of bryophyte regeneration.

All photographs Jeff Duckett

△ Figure 13. New *Pteridium* fronds after just 34 days.

Figure 14. *Ulex europaeus* seedlings after 34 days.

Both photographs Jeff Duckett

The 2020 recolonisation pattern, summarised in Table 2, clearly shows that vascular plants reappeared and recovered much faster than the bryophytes. Rapid greening of *Molinia* after only two weeks and extensive production of new *Pteridium* fronds after only four were particularly dramatic (Figs 12, 13). Crops of seedlings, all germinating at the same time for individual species with no additions at later dates, were also evident soon after the fire (Fig. 14). Sprouting from most burnt stumps of *Betula*, *Salix* and *Ulex*, but never from *Pinus*, occurred soon after the fire, with those from *Ulex europaeus* flowering within 142 days.

The first bryophyte arrivals on the dry heath were *Campylopus pyriformis* (Fig. 15) and *Funaria*, both with abundant gemmiferous protonema (Duckett & Ligrone, 1992), and *Polytrichum juniperinum* after 56 days. These were joined by *Bryum dichotomum*, *Ceratodon* and *Polytrichum formosum* after 104 days by which time *Funaria* had abundant inflorescences (Fig. 16). These were first seen on *Ceratodon* after 142 days but were infrequent. Scattered patches of *Funaria* with sporophytes of different ages (Fig. 17) were common after 186 days, whereas all the *Ceratodon* sporophytes were at the young seta stage (Fig. 18). *Polytrichum juniperinum* became more and more frequent (Fig. 19) and by 187 days had formed extensive carpets (Fig. 20).

On the wet heath the first sign of recovery

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Table 2. Bryophyte and vascular plant succession at Thursley since the fire on 20 May 2020.

| Date of recording (days after fire) | | | | | | | |
|-------------------------------------|---|--|---|---|--|--------------------------|---------------------------|
| | 17 June (18 days) | 3 July (34 days) | 22 July (56 days) | 8 September (104 days) | 16 October (142 days) | 1 December (186 days) | 15 December (202 days) |
| Vascular plants | | | | | | | |
| <i>Betula pubescens</i> | Sprouting around bases of burned saplings | As previous | As previous | As previous | As previous | Dead leaves | As previous |
| <i>Calluna vulgaris</i> | - | - | - | Sprouting from bases of burnt plants. Seedlings | As previous | As previous | As previous |
| <i>Carex arenaria</i> | - | - | New shoots from pre-existing rhizomes | As previous | As previous | As previous | As previous |
| <i>Eleocharis palustris</i> | - | - | New leaves from pre-existing clumps | As previous | As previous | As previous | As previous |
| <i>Erica cinerea</i> | - | - | - | Sprouting from bases of burnt plants. Seedlings | As previous | As previous | As previous |
| <i>E. tetralix</i> | - | - | - | Sprouting from bases of burnt plants. Seedlings | As previous | As previous | As previous |
| <i>Molinia caerulea</i> | New leaves from pre-existing clumps | Abundant new leaves from pre-existing clumps | As previous | As previous | As previous | Dead leaves | As previous |
| <i>Pteridium aquilinum</i> | - | Young fronds | Mature fronds | Mature fronds | Autumnal dying of fronds | Dead fronds | As previous |
| <i>Rumex acetosella</i> | - | - | Seedlings | As previous | As previous | As previous | As previous |
| <i>Salix spp.</i> | - | Sprouting around bases of burned saplings | As previous | As previous | As previous | Dead leaves | As previous |
| <i>Trichophorum germanicum</i> | - | New leaves from pre-existing clumps | As previous | As previous | As previous | As previous | As previous |
| <i>Ulex europaeus</i> | - | Sprouting around bases of existing plants. Seedlings | As previous | As previous | Flowering of shoots from base of existing plants | As previous | As previous |
| <i>U. minor</i> | - | - | Sprouting around bases of existing plants | As previous | As previous | As previous | As previous |

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| Date of recording (days after fire) | | | | | | | |
|-------------------------------------|----------------------|---------------------|--|---|---|---|---------------------------|
| | 17 June (18 days) | 3 July (34 days) | 22 July (56 days) | 8 September (104 days) | 16 October (142 days) | 1 December (186 days) | 15 December (202 days) |
| Bryophytes (dry heath) | | | | | | | |
| <i>Bryum dichotomum</i> | - | - | - | Occasional gemmiferous shoots. From spores | As previous | As previous | As previous |
| <i>Campylopus pyriformis</i> | | - | Small colonies in shallow depressions. Mostly protonemal. From tubers? | Extensive colonies in damp depressions with abundant caducous leaves | As previous | As previous | As previous |
| <i>Ceratodon purpureus</i> | - | - | - | Scattered shoots. Gemmiferous protonema. From spores | Scattered patches. Occasional inflorescences | Scattered patches. Occasional young capsules | As previous |
| <i>Funaria hygrometrica</i> | - | - | Numerous small patches. Gemmiferous protonema. From spores | Extensive patches. Numerous inflorescences | Extensive patches. Occasional young sporophytes | Extensive patches. Frequent sporophytes of different ages | As previous |
| <i>Polytrichum formosum</i> | - | - | - | Occasional small patches. Vegetative. From rhizomes | Frequent patches. Vegetative | As previous | As previous |
| <i>P. juniperinum</i> | - | - | Occasional rhizomes | Frequent patches. Vegetative. From rhizomes | Extensive lawns. Vegetative | As previous | As previous |
| Bryophytes (wet heath) | | | | | | | |
| <i>Sphagnum compactum</i> | - | - | - | Occasional green capitula | Numerous green capitula | As previous | As previous |
| <i>Polytrichum commune</i> | - | - | - | Extensive patches on and between <i>Molinia</i> tussocks. Vegetative. From rhizomes | As previous | As previous | As previous |
| <i>Marchantia polymorpha</i> | - | - | - | Highly gemmiferous thalli. From spores | As previous | Occasional carpocephala | Numerous carpocephala |

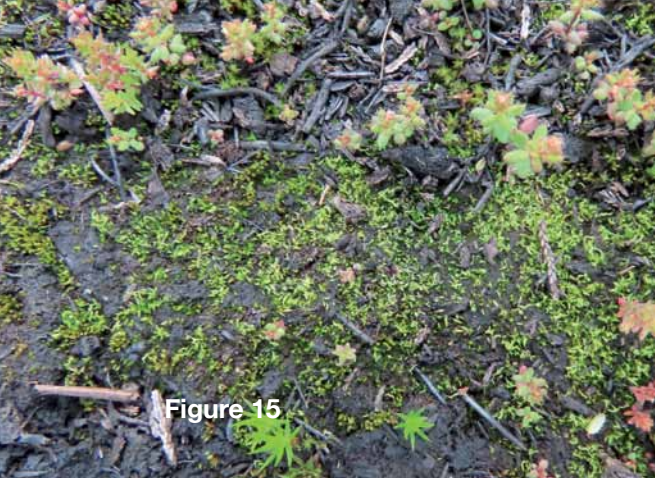


Figure 15



Figure 16



Figure 17



Figure 18



Figure 19



Figure 20

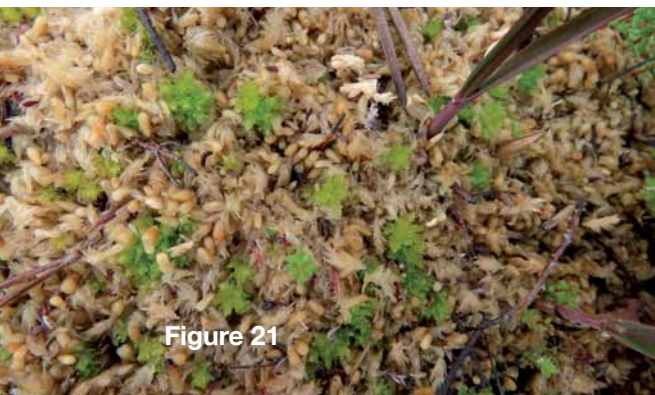


Figure 21



Figure 22

- < Figure 15. *Campylopus pyriformis* after 104 days.
Figure 16. Male shoots of *Funaria* and sterile *Ceratodon* after 142 days.
Figure 17. *Funaria* with sporophytes of different ages after 142 days, growing with *Erica* seedlings.
Figure 18 *Ceratodon* (left) and *Funaria* (right) with very young sporophytes after 186 days.
Figure 19. Rapidly increasing *Polytrichum juniperinum* after 104 days.
Figure 20. Carpets of *Polytrichum juniperinum* after 184 days.
Figures 21 and 22. *Sphagnum compactum* regenerating after 104 and 184 days.

All photographs Jeff Duckett

was the appearance of new capitula after 104 days (Figs 21, 22) on seemingly dead *Sphagnum compactum* (Fig. 12). By 202 days, over 25% of the apparently dead hummocks immediately after the fire had re-greened completely. Dry hummocks of *Polytrichum commune* appeared to be completely burnt out by the 2020 fire (Fig. 23). However, new shoots of *Polytrichum commune*, particularly in damp hollows (Fig. 24) and much less frequently on tussocks, were in evidence after 186 days. As with the *P. juniperinum* and *P. formosum*, on the dry heath, all the new shoots were vegetative.

Unlike post-2006, the reappearance of *Marchantia* in 2020 was restricted to the wet heath. It was most extensive on the former *Campylopus brevipilus*/*C. introflexus* experimental site. Here, on the 15 December visit, many of the thalli were completely submerged. Initially, after 104 days, the *Marchantia* comprised highly gemmiferous, purely vegetative thalli (Fig. 25) and the first fertile plants were not seen until 186 days (Fig. 26). A noticeable feature of the young thalli is that they ceased gemma production before carpocephalum formation (Fig. 27). In 2020 the vast majority of the fertile plants were male (Table 3). An aggregation of over 200 male thalli (Fig. 28) was the largest single sex cluster

that we encountered at Thursley, although after the 2006 fire aggregations of 20 or more thalli of the same sex were not uncommon (Fig. 29).

The other place with numerous *Marchantia* thalli in 2020, but not noted post-2006, was between and on the sides of burned *Molinia*/*Polytrichum commune* tussocks (Fig. 30).

Discussion

In 2020, the most notable absence from the characteristic post-fire specialists (Blockeel *et al.*, 2014) was *Leptobryum pyriforme*, also uncommon in 2006-2020, whereas an abundance of *Poblia nutans* (Fig. 7) two and three years after the 2006 fire is very much in line with other British heathlands (Coppins & Shimwell, 1971; Southorn, 1976; Hobbs & Gimingham, 1987; Burch, 2009). Surprisingly it is not mentioned by Atherton *et al.* (2010) and Blockeel *et al.* (2014) in connection with fires nor by Gardiner (1981) in his Surrey flora.

Phenological considerations

Our new observations now provide a clearer picture of the temporal succession of different species after fire and of the effects of fire on reproductive cycles. Vascular plants are the first to show signs of recovery (Figs 12, 13) whilst *Funaria*, *Campylopus pyriformis* and *Polytrichum juniperinum* have a head start as the earliest bryophyte arrivals (Figs 15, 19), with *Marchantia* appearing some 50 days later (Fig. 25). *Funaria* stands apart from all the other mosses as it produced waves of sporophytes in the same year, 2020 (Fig. 17), whereas one crop of late autumn young sporophytes in *Ceratodon* (Fig. 18) is in line with one cycle of spring-maturing sporophytes in 2021, and conforms with annual reproductive cycles in many, if not most, mosses (Duckett & Pressel, 2017).

Our 2020 observations perhaps provide the



Figure 23



Figure 24



Figure 25



Figure 26



Figure 27



Figure 28



Figure 29



Figure 30

- ◁ Figure 23. A burnt out, dead *Polytrichum commune* hummock 56 days after the 2020 fire.
Figure 24. Burnt out *Polytrichum commune*/*Molinia* hummocks with *Polytrichum commune* only regenerating between them after 202 days.
Figure 25. Colony of *Marchantia* covered with gemma cups; 186 days.
Figure 26. Male and female *Marchantia* colonies growing side-by-side after 186 days.
Figure 27. Prior to sex organ formation *Marchantia* thalli cease gemma production; after 186 days.
Figure 28. An aggregation of more than 200 male colonies of *Marchantia* over 1 m in diameter in December 2020.
Figure 29. An aggregation of 20 female colonies of *Marchantia* in June 2008.
Figure 30. *Marchantia* colonizing a dead *Polytrichum commune*/*Molinia* hummock after 202 days.

All photographs Jeff Duckett

best evidence to date that polytrichaceous mosses survive fires via their underground rhizome systems, mirroring *Pteridium* but on a miniature scale. This was expected for *P. commune* as the rhizomes always grow in standing water, even with the plants forming large hummocks, but is remarkable for *P. formosum* in the top 3 cm of peaty soil and especially so for *P. juniperinum*, scarcely 1 cm below the surface.

The biggest effect of fire on these polytrichaceous mosses is the disruption to their annual reproductive cycles. After the 2006 fire it was not until spring 2007 that *P. juniperinum* and *P. formosum* produced their first inflorescences and the first sporophytes appeared in 2008. For *P. commune* this was a year later. Thus, in the autumn of 2021 we might expect inflorescences on *P. juniperinum* and *P. formosum*, but none on *P. commune* until 2022 and the first sporophytes not until 2023.

The biggest long-term loser to fires at Thursley is *Campylopus brevipilus* (Fig. 10). One major factor is almost certainly its restricted spreading at Thursley by deciduous leaves (but on a much

more limited scale compared to *C. pyriformis*) and fragile leaf tips and not via tubers and spores. *C. brevipilus* became much rarer in the 2006 burnt areas than before the fire. The same will almost certainly be the case long after the 2020 fire following the destruction of its optimum site.

Whereas the provenance of the aforementioned post-fire species is readily explained, the early appearance of *Campylopus pyriformis* is more problematic since it only rarely produces sporophytes in Britain (Blockeel *et al.*, 2014), and none have been recorded at Thursley. Large-scale blowing or washing in of caducous leaves from non-burnt areas seems improbable, with regeneration from tubers far more likely. In *C. pyriformis*, colourless, multicellular, long cylindrical rhizoidal tubers, 300–700 µm long have been reported elsewhere in western Europe, North America and from the southern hemisphere (Arts, 1987; Risse, 1988; Arts & Frahm, 1990; Ochyra *et al.*, 2008), but not in Britain, where they have only been seen in cultured material (Blockeel *et al.*, 2014; Pressel & Duckett, unpublished). Thus a detailed examination of the rhizoid system of *C. pyriformis* is now overdue, with the rapid appearance of this species after an absence of nearly a decade at Thursley attesting to the putative longevity of the tubers. It is also noteworthy in this context that we found no evidence of any kind of direct regeneration of burnt *C. introflexus*, a species where subterranean propagules have never been described.

The biggest difference between the two burns was the much more rapid recovery of *Sphagnum compactum* and the much more restricted distribution of *Marchantia* in 2020. A possible explanation for the former is the much wetter conditions at Thursley in the latter part of 2020. Indeed, this is the first year when we have seen *Marchantia* under water. The most likely factor that restricted the distribution of *Marchantia* was

probably the lack of rain in the spring of 2020. Though April–June is the optimal period for spore release in *Marchantia* (Pressel & Duckett, 2019), this might have been depressed in 2020 as these months were particularly dry.

A final notable feature of the temporal data on *Funaria* and *Marchantia* is that their life cycles are much more protracted in nature than in culture. From spore germination to spore release it took a minimum of 140 days in *Funaria* and 186 days in *Marchantia* at Thursley in 2020, compared with 65–90 days in culture (Krupa, 1969; Garner & Paolillo, 1973; Bowman *et al.*, 2016). These differences are almost certainly due to dry periods which arrested the growth of the wild plants.

Sex ratios

Whereas one and two years after the 2006 fire the Thursley *Marchantia* population had a 1:1 sex ratio, with a slight male bias, a huge majority of the fertile 2020 plants were male (Table 3). A recent study of *Marchantia inflexa* populations from the Caribbean and Southern USA (Stieha *et al.*, 2014) goes some way to providing an explanation. In *M. inflexa*, male plants produce gemmae earlier and in greater profusion than do the females. If the same is true in *M. polymorpha* we might expect a predominance of male plants during early colonisation. Were this the case then the sheer abundance of gemmae on many of the very young Thursley *Marchantia* thalli suggests that they could indeed have been male. In addition, the aggregations of male-only colonies, sometimes containing over 200 individual plants, suggests that these most likely originated from single gemmae with the very wet conditions in 2020 facilitating dispersal. Re-examination of our images from 2007, showing unisexual aggregations of up to 20 individuals, also suggests single gemma origins.

In bryophytes, mature populations of dioicous

species are typically female-biased. The variety of explanations proposed for such skewed sex ratios range from environmental factors to sex-specific traits in life histories (Longton & Schuster, 1983; McLetchie, 1992; Shaw & Gaughan, 1993; McLetchie & Puterbaugh, 2000; Bowker *et al.*, 2000; Cronberg *et al.*, 2006; Crowley *et al.*, 2005; Bisang *et al.*, 2006, 2015; Glime, 2007; Hedenäs *et al.*, 2010; Horsley *et al.*, 2011; Rydgren *et al.*, 2006, 2010; Stark *et al.*, 2010; Baughman *et al.*, 2017; Bisang & Glime, 2017).

A female bias has been reported in *Marchantia* populations from as far apart as windswept open habitats in the Falkland Islands (*M. berteriana*, Engels, 1980; Duckett *et al.*, 2012) to tropical forests in Puerto Rico (*M. chenopoda*, Moyá, 1992) and Trinidad (*M. inflexa*). As a result of exhaustive observational, experimental and modelling studies, the female bias in *M. inflexa* is attributed to a faster growth rate and lower gemma production by the females (McLetchie & Puterbaugh, 2000; McLetchie *et al.*, 2002; Fuselier & McLetchie, 2002, 2004; Crowley *et al.*, 2005; Garcia-Ramos *et al.*, 2007; Groen *et al.*, 2010; Stieha *et al.*, 2014). It is therefore interesting that at Thursley we found a slight but constant male-biased sex ratio (Table 3). Though we did not record actual numbers of gemma cups on plants of different sexes nor the sizes of

Table 3. Sex ratios in *Marchantia polymorpha* at Thursley Common. The numbers represent approximately 10–20% of total populations in 2007 and 2008 and all the fertile colonies in 2020.

| Date | Number of individuals | | Female/male |
|------------------|-----------------------|-------|-------------|
| | Female | Male | |
| May 2007 | 68028 | 73016 | 0.93 |
| June 2007 | 44481 | 50058 | 0.89 |
| May 2008 | 68009 | 74749 | 0.91 |
| June 2008 | 41718 | 47295 | 0.88 |
| 1 December 2020 | 1 | 35 | 0.03 |
| 15 December 2020 | 23 | >200 | < 0.12 |

individual plants, it is clearly apparent from our analysis of over 100 images that there were no differences between the sizes of male and female plants but the males were less branched than the females and produced fewer gemma cups and carpocephala (10 on males 10 cm in diameter compared with 15-20 in females the same size). Possible explanations for the excess of males at Thursley may lie in the high nutrient status favouring their early establishment in a uniform habitat or the higher cost of sporophyte versus spermatozoid production or better survival of the males over the winter period.

Other examples of male bias and possible explanations include the following: sexual dimorphism and male-biased mortality in the desert moss *Syntrichia caninervis* (Baughman *et al.*, 2017), differences in stress tolerance favouring males in *Mnium hornum* (Newton, 1972), differences in the timing of gametangia production and different conditions for male and female development in *Lophozia ventricosa* var. *silvicola* (Laaka-Lindberg, 2005). In the aquatic liverwort *Scapania undulata* this is considered to be a strategy to overcome sperm dilution and ensure fertilisation over longer distances in water (Holá *et al.*, 2014), whilst no explanation is offered for the male bias in the Brazilian rainforest epiphyllous moss *Crossomitrium patrisiae* (Alvarenga *et al.*, 2013).

2021 and beyond

Looking to later in 2021 it will be interesting to see if female *Marchantia* plants catch up with the males. In addition, since male inflorescences of *Ceratodon* are readily distinguishable in the autumn, 2021 will provide a golden opportunity to investigate the sex ratio for the first time in this dioicous species: we have simply no idea whether or not this will conform with the female bias found in the majority of mature moss populations. In a

similar vein possible differences between male and female *Ceratodon* plants in culture have yet to be investigated despite its development as a model moss alongside *Physcomitrium patens* (Thornton *et al.*, 2005; Szóvényi *et al.*, 2015) including a detailed analysis of its sex chromosomes (McDaniel *et al.*, 2013).

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