

Received: 10 November 2020 | Revised: 7 April 2021 | Accepted: 12 April 2021

DOI: 10.1111/jvs.13033

## RESEARCH ARTICLE

Journal of Vegetation Science



# Rapid post-fire re-assembly of species-rich bryophyte communities in Afroalpine heathlands

Kristoffer Hylander<sup>1</sup>  | Carl Alexander Frisk<sup>2</sup> | Sileshi Nemomissa<sup>3</sup> |  
Maria Ulrika Johansson<sup>1</sup> 

<sup>1</sup>Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden

<sup>2</sup>School of Science and the Environment, University of Worcester, Worcester, UK

<sup>3</sup>Department of Plant Biology and Biodiversity Management, Addis Ababa University, Addis Ababa, Ethiopia

## Correspondence

Kristoffer Hylander, Department of Ecology, Environment and Plant Sciences, Stockholm University, 106 91 Stockholm, Sweden.  
Email: [kristoffer.hylander@su.se](mailto:kristoffer.hylander@su.se)

## Funding information

Funding for this project was provided by Formas [231-2013-1973 to MUJ] and from SIDA [minor field study to CAF].

**Co-ordinating Editor:** Rune Halvorsen

## Abstract

**Questions:** In some fire-prone ecosystems, bryophytes play a crucial role by providing the surface fuel that controls the fire return interval. Afroalpine heathlands are such an ecosystem, yet almost nothing is known about the bryophytes in this system. We do not know the level of species richness, or if there is a successive accumulation of species over time, or if some species are adapted to specific phases along the successional gradient, for example early-successional species sensitive to competition.

**Location:** Afroalpine heathlands in Ethiopia.

**Methods:** We made an inventory of all bryophytes in 48 plots of 5 m × 5 m, distributed along a chronosequence from 1 to 25 years post fire. The heathlands are located between 3500 m and 3800 m a.s.l. and are managed by traditional pasture burning with fire intervals of 8–20 years.

**Results:** We found in total 111 taxa of bryophytes. Post-fire mortality was almost 100%. The youngest plots had only a few cosmopolitan species often found after fire. Initially, species richness increased monotonically while starting to level off around 15 years after fire, when many plots had around 30 species and a high cover of *Breutelia diffracta*, which is a key ground-living species, important as surface fuel. Most species were found with sporophytes, a pattern even stronger for the most frequent species.

**Conclusions:** Interestingly, bryophyte diversity is already remarkably high by only 15 years after total eradication. The relatively slow accumulation of species in the first years after fire suggests that dispersal in space, and not time, is the major mechanism by which sites regain their diversity (i.e. spore banks play a smaller role than colonization of wind-borne spores). This indicates that the high species richness is built up through colonization from surrounding heathlands, and perhaps also from higher-altitude alpine grasslands and lower-altitude forests, and that the bryophyte diversity in this system is maintained by the traditional fire and grazing management.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *Journal of Vegetation Science* published by John Wiley & Sons Ltd on behalf of International Association for Vegetation Science.

## KEYWORDS

chronosequence, colonization, disturbance, Ethiopia, liverwort, moss, species assembly, succession

## 1 | INTRODUCTION

Fire plays an important role in driving evolution and patterns of plant diversity in many ecosystems around the world (Bond & Keeley, 2005). A classic example is the shrub-dominated vegetation found in Mediterranean climates, where large numbers of species are adapted to early successional stages after fire (Keeley et al., 2012). However, fire also plays an important role in regulating species composition in tropical, temperate and boreal ecosystems, both in natural and human-modified landscapes (Bond-Lamberty et al., 2007; Lehmann et al., 2014). There is a large variation in plant diversity as well as in successional patterns after fire among ecosystems that regularly burn, explained by variations in evolutionary history of the species pool, fire ecology, dispersal traits and human impact (Keeley et al., 2005; Tucker & Cadotte, 2013; Mittelbach & Schemske, 2015). To develop sustainable management practices, especially in an increasingly changing world, it is important to understand the patterns and processes behind this variation (Chang & Turner, 2019).

Bryophytes are often abundant, biologically diverse and ecologically important in ecosystems where fire is rare, such as in tropical cloud forests, wetlands, alpine and oceanic/maritime habitats (Turetsky et al., 2012; Fenton et al., 2015). Additionally, they also play a crucial ecological role in some fire-prone ecosystems by providing the surface fuel that carries fires. For example, in boreal forests large feather mosses or lichens build up a thick continuous bottom layer which controls the fire return intervals (Schimmel & Granström, 1997; Riccardi et al., 2007). Bryophytes also occur with varying cover and diversity in many other fire-prone ecosystems, even when they do not drive the fire return interval (Esposito et al., 1999).

Little is known about the role of fire in bryophyte evolution (Waters et al., 2011), even if the general patterns indicate that bryophytes are killed by fires and that the early successional stages are dominated by a few wind-dispersed cosmopolitan species. This is the case in a wide range of ecosystems, such as boreal forests in North America (Rees & Juday, 2002) and Europe (Ryömä & Laaka-Lindberg, 2005), Mediterranean macchia (Esposito et al., 1999) and *Eucalyptus* forests in Australia (Pharo et al., 2013). However, the possible role of a bryophyte spore bank in post-fire community assembly needs to be studied in more ecosystems. For example, in the South African fynbos there are many bryophyte species with traits suggesting adaptations to dispersal in time (between dispersal events) rather than space (e.g., few large spores in such genera as *Gigaspermum*, *Archidium* and *Riccia*; Magill, 1987; Perold, 1999). This suggests that the spore bank may play a role in recolonization after disturbance for such species, since the spores generally are deposited very close to the mother plant and that the disturbance regime is characterized by regularly recurrent fires. Although the exact mechanism is uncertain, at least one study has

provided an example of regeneration from spore banks after fire in a North American desert community (Smith et al., 2014). Studies investigating post-fire succession often find a rather slow return of the pre-fire bryophyte species composition. For example, soil crusts including bryophytes and lichens often need several decades to recover (Johansen, 2001) and the diversity of bryophytes in a boreal forest peaked 276 years after fire in eastern Canada (Fenton & Bergeron, 2008). To what extent the succession is driven by species dispersing in time (spore banks) is an important research field (Smith et al., 2014), as is the role of adjacent undisturbed habitats, or fire refugia, as sources for recolonizing propagules (Hylander, 2009; Wills et al., 2018). Long-distance dispersal has been assumed to be rare in most bryophytes (Barbé et al., 2016). However, several recent studies have suggested that dispersal over distances greater than a few kilometres can be important even for local community assembly in some bryophyte species (Hutsemékers et al., 2008; Lönnell & Hylander, 2018).

In moist temperate climates, heathlands are generally nutrient-poor environments dominated by ericoid shrubs of varying sizes. Their existence is in most cases closely associated with a long history of human management of fire to improve grazing land, even if, e.g., cold climates also partly explain the lack of trees in these systems (Mallik, 1995; Johansson & Granström, 2014). Most heathlands burn regularly, and a closed and thick cover of bryophytes (mostly mosses) often plays an important role as surface fuel for carrying the fire (Schimmel & Granström, 1997). Heathlands of western Europe do not have as high a species diversity of bryophytes as otherwise comparable systems, and the early successional stages are dominated by cosmopolitan species with small spores that are easily dispersed over long distances (Maltby et al., 1990).

Tropical mountains often have a zone of heathlands or similar vegetation above the tree line (Spehn, 2006). In Africa, this zone is often pronounced and wide due to recurrent man-made fires to enhance pasture quality (Hedberg, 1964; Wesche et al., 2000). *Erica*-dominated heathlands of East Africa are likely to have a long history of recurrent fires (>11,000 years, Schuler et al., 2012; Gil-Romera et al., 2019) along with a high diversity of vascular plants (Johansson et al., 2018; Peters, 2019). Many vascular plants survive the fires through underground structures or recolonize fast with fire/grazing management regimes which allow species from higher elevations to expand their ranges downslope (Johansson et al., 2018). Like European heathlands and boreal forests, large fluffy mosses play a crucial role for the fire dynamics in Afroalpine heathlands (Johansson & Granström, 2014). When 10–20 year old *Erica* stands burn, they generally have a thick bottom layer of large mosses, dominated by *Breutelia diffracta* (Johansson & Granström, 2014). However, little is known about the diversity of bryophytes in these heathlands, how it varies along the successional gradient and to what extent early successional stages contain unique species (Miehe & Miehe, 1993, 1994).

The overall aim of this study is to describe the bryophyte species' compositional change after fire in Afroalpine heathlands. We asked the following questions:

1. *Overall species richness*: how does species richness vary with time since fire?
2. *Species compositional changes*: which explanatory variables, including time since fire, control species composition? Is there any turnover in species composition along the succession? Do any bryophyte species regularly survive fires? Are there unique species confined to newly burnt sites?
3. *Functional groups, dispersal traits and keystone species*: how do richness of different functional groups vary with time since fire? What dispersal traits characterize species typical of the different successional stages? How does the cover of *Breutelia diffracta* (which is a key species for transmitting fires) build up over time after fire?

We investigated these questions using a chronosequence after fire of 48 plots varying in time since fire from one year to 25 years in heathlands of the Bale Mountains, SE Ethiopia.

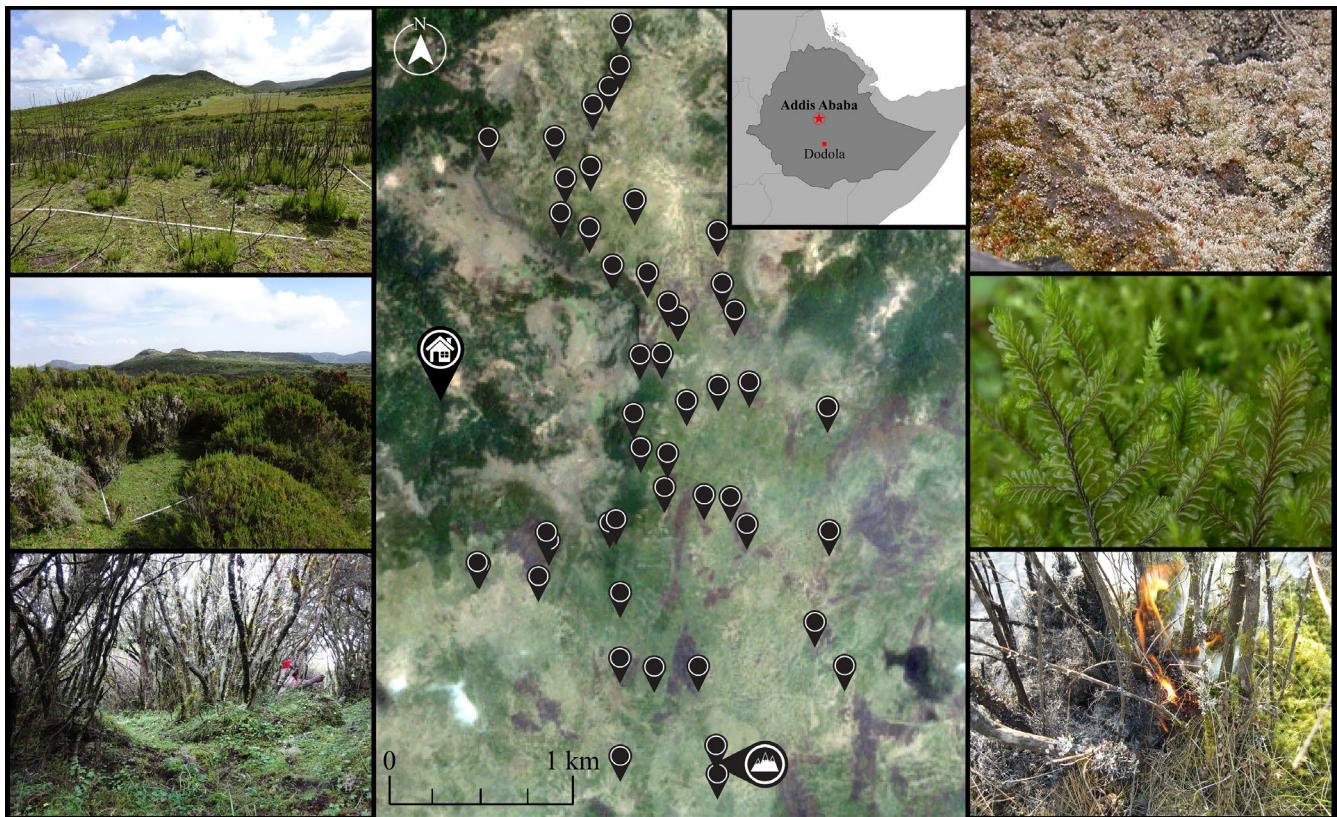
By answering these questions, we can better understand the dynamics of bryophyte diversity in relation to fire. Such knowledge can complement knowledge about other organism groups (e.g., vascular plants, mammals, birds) and may be useful for evaluation of

the impact of current land use on biodiversity and for guiding future conservation management (Chang & Turner, 2019).

## 2 | METHODS

### 2.1 | Study system

The study was conducted in the Bale Mountains in SE Ethiopia, south of the town of Dodola (6.832328° N, 39.247421° E, coordinates are for the 3,711-m peak at the bottom of Figure 1). The area is characterized by montane forests, on the northern aspect dominated by *Juniperus procera* up to ca 3,100 m a.s.l., and by *Hagenia abyssinica* and *Hypericum revolutum*-dominated forests up to 3,300 m a.s.l. The next-higher vegetation zone, often referred to as the ericaceous belt, could ecologically be divided into two distinct zones. The lower part is dominated by tree-forming *Erica trimera*. Above the tree line, at ca 3,450 m a.s.l., this species is one of two dominating shrubs, here having a multistemmed structure, up to 3 m in height, and growing together with similarly-shaped *Erica arborea* (Friis, 1986; Johansson & Granström, 2014). These shrubby heathlands dominate up to 3,900 m a.s.l. It was in this zone that we conducted our study. The climate is characterized by a long rainy season from March to November while the driest period, from December to February, sometimes extends



**FIGURE 1** Map of the study area in the Bale Mountains south of Dodola with all inventoried plots indicated with a black dot. Angafu field station and the highest peak are indicated with symbols (house and mountain, respectively). Inset: map of location in Ethiopia. Left pictures from top: young, intermediate and old stands. Right pictures from top: the moss *Bryum argenteum* typical on soil in newly burnt stands, the liverwort *Plagiochila squamulosa*, a typical epiphyte in old stands, and fire burning in the dense carpet of the moss *Breutelia diffracta*

into April. At 3,400 m a.s.l., the precipitation is around 1,740 mm per year and average maximum and minimum temperatures are 15°C and 5°C respectively (Johansson & Granström, 2014). The heathlands are managed primarily for cattle grazing by an intricate system of burning of old *Erica* stands that over time has created a mosaic landscape of stands in different successional stages (Johansson et al., 2019). Young (1–4-year-old) grass-dominated stands are preferred by the livestock (Gustafsson, 2009). The typical fire behaviour is afternoon, uphill-moving, high-intensity crown fires, with 3–10 m long flames, consuming all surface fuels and all fine fuels in the shrub canopies. Soil impact is generally minor, because the humus layer is rarely dry enough to burn (Johansson et al., 2012). Burn sizes in this area are typically 1–100 ha (Johansson et al., 2019).

## 2.2 | Study design and data collection

In an area of 20 km<sup>2</sup>, we established 48 plots of 5 m × 5 m in a representative area of stands of different ages (time since last fire; the design covers 17 different fire years and each stand normally had only one plot – for more details on site selection see Johansson et al., 2018; Figure 1). In each of the 48 plots, we recorded all bryophyte species. We took samples from all different substrates such as soil, boulders, *Erica* stems and twigs across the whole plot. The samples were identified to species, or in some cases morpho-species, in the lab (see *Acknowledgements* for a list of experts who have verified or identified some specimens). Voucher specimens are placed in ETH (National Herbarium of Ethiopia, Addis Ababa University). The taxonomy follows Wigginton (2009) for liverworts and O'Shea (2006) for mosses. Time since last fire was assessed for each plot by a combination of an established correlation between *Erica* height and age based on counts of annual rings (Johansson et al., 2012), burn maps of the area (M. Johansson and A. Abraham, unpublished results), satellite images and the structure of the *Erica* shrubs (see details in Johansson et al., 2018). In each plot we estimated bare soil cover and the cover of a specific large, ground-living moss, *Breutelia diffracta*, which is an important surface fuel. We also measured the total cover of *Erica* and the average height of *Erica trimera* shrubs and multiplied these measures to get an index of shade in the plots (here after referred to as “Shade index”). Altitude and position were measured using a handheld GPS (for mean and range of values of explanatory variables, see Appendix S1).

## 2.3 | Classification into different functional groups

Species were classified into the following six functional groups based on taxonomy, main substrate (ground or epiphytic) and whether or not they were found with sporophytes at any occasion: liverworts on soil; epiphytic liverworts; epiphytic mosses; pleurocarpous (i.e. mat-forming) mosses on soil; acrocarpous (i.e. cushion- or turf-forming) mosses on soil with sporophytes; and acrocarpous mosses on soil without sporophytes.

## 2.4 | Statistical analyses

All analyses were done using R version 3.6.1. (R Core Team, 2019) and residual plots for models were inspected to evaluate deviations from statistical assumptions.

To test if the total species richness changed with time since fire, we performed a linear regression with time since fire as the explanatory variable.

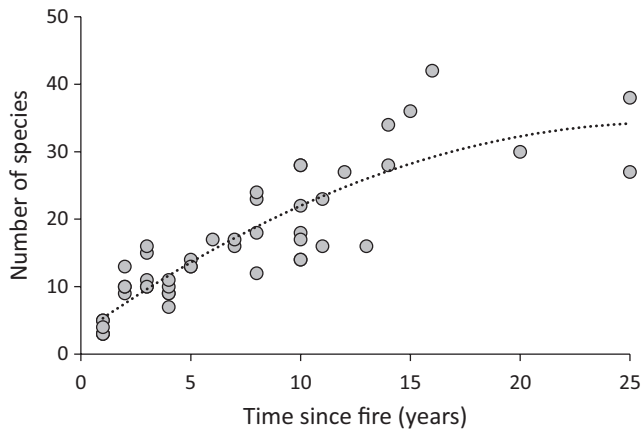
To explore the overall species compositional variation across time since fire and other environmental and biotic gradients we conducted a non-metric multidimensional scaling (NMDS) ordination of a species-by-site matrix with presence/absence data for all species in the 48 plots. We set the model parameter of the ordination to two axes ( $k = 2$ ) and 100 iterations (trymax = 100) using the metaMDS function. To test if the variation in species composition was related to time since fire, shade index, bare soil cover, cover of *Breutelia* and altitude we ran a multivariate ANOVA (using the Adonis2 function of R). Prior to analysis we log-transformed all variables except altitude. Since time, the shade index and the cover of *Breutelia* were strongly correlated (see Appendix S1), we ran a model with only three variables: time since fire, bare soil cover and altitude. We also plotted the site scores in the NMDS ordination plot and superimposed significant relationships to explanatory variables in the same graph using the envfit function. All multivariate analyses (metaMDS, Adonis2 and envfit) were performed by use of the *vegan* package in R (Oksanen et al., 2019). We found a few shoots of surviving larger mosses from the pre-burn stage in two of the young plots (see section 3 *Results*). These records were omitted from the species compositional analyses.

To illustrate how the species richness in different functional groups varied along the chronosequence we performed LOWESS (locally weighted scatterplot smoothing) regressions with time since fire as explanatory variable. We set the  $f$ -value to 0.5 (regulating how large a proportion of data is included in the calculation of the slope at each point). To examine the role of spore dispersal in the colonization process we regressed the proportion of species that were found with sporophytes against time since fire (log-transformed) using a Generalized Linear Model (GLM) with a binomial error distribution. We also tested if species that were found with sporophytes were more frequent than species not found with sporophytes using a chi-squared test.

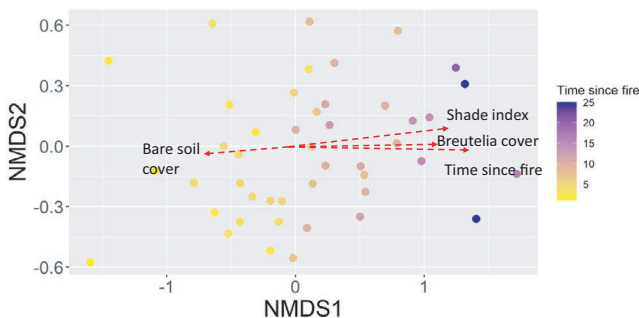
## 3 | RESULTS

### 3.1 | Species richness

In total we recorded 111 taxa (95 mosses and 16 liverworts; Appendix S2). The number of species per plot (5 m × 5 m) varied from 3 to 42 and increased sharply with time since fire ( $p < 0.001$ ,  $r^2 = 0.72$  in a linear regression), with a tendency to level off at ages above 15 years (Figure 2).



**FIGURE 2** Number of bryophyte species in 5 m × 5 m plots as a function of time since fire. A polynomial trendline is superimposed ( $r^2 = 0.77$ )



**FIGURE 3** Non-metric multidimensional scaling (NMDS) ordination of 48 sites along a chronosequence of time since fire. Fitted environmental variables ( $p < 0.05$ ) superimposed on the ordination (see Appendix S1). Stress = 0.13

### 3.2 | Species compositional changes

The variation in species composition between plots was strongly related to time since fire ( $F_{1,44} = 41.6$ ,  $p = 0.001$ ) and bare soil cover ( $F_{1,44} = 8.1$ ,  $p = 0.006$ ), but not to altitude ( $F_{1,44} = 1.3$ ,  $p = 0.23$ ) in the multivariate Adonis2 analysis. Shade from the dominant *Erica* shrubs and the cover of the ground moss *Breutelia diffracta* correlated strongly with time since fire (Figure 3, Appendix S1).

Most species were recorded more frequently in older stands (Figure 4, Appendix S1), but there was also a turnover component with a few species with their main occurrences in young or intermediate successional stages (Figure 4, Appendix S2). Some typical examples of distribution patterns of individual species are shown in Figure 5.

We only found very limited survival of species in the newly burnt plots. Very small amounts of one species, *Breutelia diffracta*, were found in one plot and in one plot we found a few shoots of *Anacolia laevisphaera* and *Leptodontium capituligerum* that seemed to be alive (among fire-killed shoots).

Very few species were confined to newly burnt sites (Figure 4, Appendix S2). The species most strongly associated with such sites were *Funaria hygrometrica*, *Bryum argenteum*, and *Ceratodon purpureus*, all of which are cosmopolitan species that usually colonize newly disturbed (often by fire) areas in many parts of the world. The two latter species seemed to survive in trampled places many years after fire (Figure 4), even if they were dominant only in the youngest plots (Figure 1, personal observation).

### 3.3 | Functional groups, dispersal traits and key stone species

The turnover of species along the successional gradient can be illustrated by the variation in number of species in different functional groups over time (Figure 6). All epiphytic species increased monotonically with time. A similar pattern was displayed by ground-living liverworts and pleurocarpous mosses, while ground-living acrocarpous mosses showed a more varied pattern depending on their being regularly fertile or not.

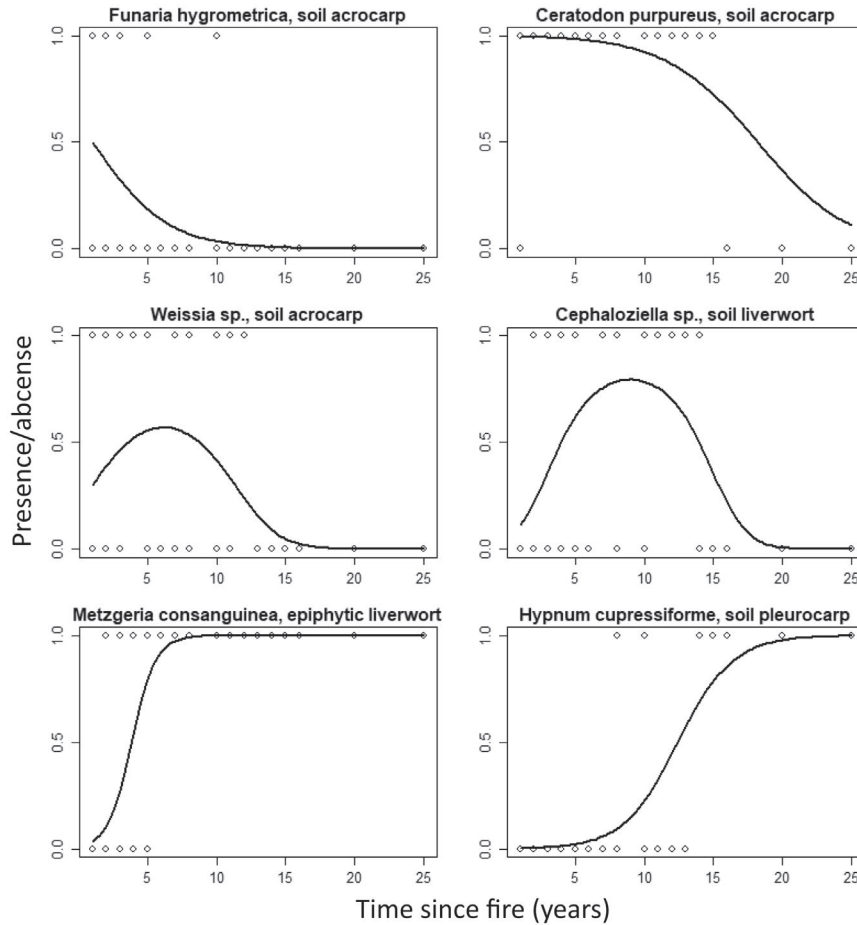
Small ground-living acrocarpous mosses that frequently produce spores dominated the early stages, while acrocarpous species not found with spore capsules showed a very similar pattern of increase with time as epiphytic mosses (up to 15 years after fire; Figure 6). The proportion of species that were found with sporophytes decreased with time since fire (Figure 7,  $r^2 = 0.30$ ,  $p < 0.001$ , log-transformed time since fire) from around 80% shortly after fire to 60% at the end of the chronosequence. Species that were found with sporophytes were on average more frequent than species not found with sporophytes ( $\chi^2 = 5.6$ ,  $p = 0.018$  when comparing frequencies 1–5 [46% with sporophytes] with 6–48 [70% with sporophytes]; see Appendix S1). However, some of the common species not recorded with sporophytes actually had plenty of asexual propagules, (e.g., *Metzgeria consanguinea*, recorded at 32 sites; Appendix S2).

The cover of *Breutelia diffracta*, the key surface fuel species, increased sharply with time since fire, perhaps with a tendency to level off at ages above 15 years (few and scattered data points above this age;  $p = 0.001$ ,  $r^2 = 0.43$ , Figure 8). Cover values above 15% were only found in plots burnt  $\geq 10$  years ago.

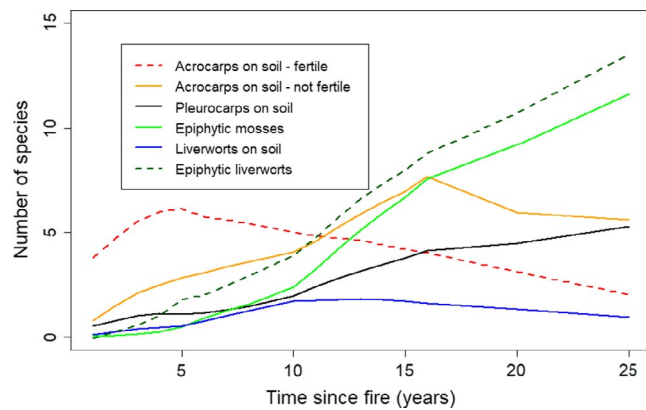
## 4 | DISCUSSION

The defining role of fire in shaping biodiversity in many ecosystems is well established (He et al., 2019). However, despite the fundamental roles of bryophytes in driving the fire dynamics by providing necessary continuous surface fuel, our knowledge of bryophyte diversity and succession in these systems is very limited. Here we show, in an Afroalpine heathland system, that typically all bryophytes are killed by fire, that the subsequent colonization most likely starts with wind-dispersed spores, and that species diversity builds up to high levels before the next fire





**FIGURE 5** Examples of distribution patterns of frequent species along the chronosequence of time since fire. Predicted lines from logistic regressions are superimposed

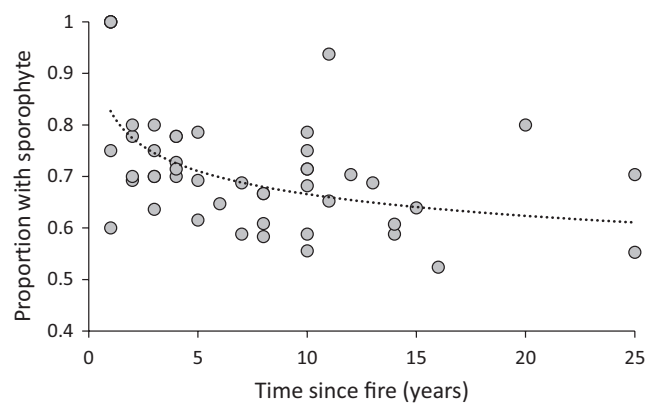


**FIGURE 6** Variation in species richness of different functional groups in relation to time since fire. LOWESS regression lines ( $f = 0.5$ )

also seems to be the most common pattern in other systems (Ryömä & Laaka-Lindberg, 2005; Pharo et al., 2013).

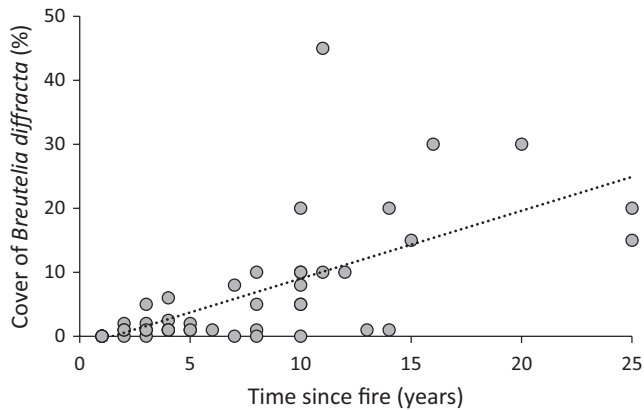
#### 4.2 | Biodiversity in dynamic mosaic systems

Time since fire, or other major disturbances, is often a strong determinant of species composition of vascular plants as well as



**FIGURE 7** Proportion of species recorded with sporophytes along the chronosequence. Trend line from log-transformed x-axis

of other organism groups (Chang & Turner, 2019). The observed pattern of change in dominant bryophyte species over time since fire in our studied heathland system thus accords with the typical successional pattern (Jean et al., 2017). In our case it was easy to identify species typical for both early-, middle- and late-successional stages. However, there is no consistency amongst the world's ecosystems in how species richness varies along the succession after disturbances, as sometimes early and sometimes later stages are the more diverse (Inouye et al., 1987; Keeley &



**FIGURE 8** *Breutelia diffracta* cover as a function of time since fire. Linear trend lines superimposed

Fotheringham, 2003). Several explanations for patterns of change in species richness along successions have been proposed, most of which invoke the evolution of special adaptations which allow species to take advantage of resources available just after fires (Keeley et al., 2005). Thus, the available species pool is central to understanding these patterns (Mittelbach & Schemske, 2015). In the Afroalpine heathlands studied here, the pattern of monotonic increase during the first 10–15 years after fire is strong. A likely explanation is the combined effect of: (i) a start from zero with no survivors and likely a small contribution from the spore bank; (ii) a steady increase in local habitat complexity (Chang & Turner, 2019); (iii) accumulation of rare colonization events (Fenton & Bergeron, 2013); and (iv) the fine-scaled patches produced by recurrent anthropogenic ignitions (Bird et al., 2008; Johansson et al., 2018). Perhaps, the management for grazing in the heathlands contributes to maintaining local disturbance and thus the possibility for early-successional species to remain longer in the system without being outcompeted by large dominant bryophyte species. It is apparent that the later stages in the succession have a large share of epiphytic species that have established in the new canopy of the growing *Erica* shrubs, as well as large dominant species (both acrocarps and pleurocarps) thriving better in the shady and trampling-free space under the shrubs than inbetween them.

It is difficult to compare species richness across studies since different researchers use different plot sizes and species accumulate differently in different systems. However, the presence of 30–40 bryophyte species in a 25-m<sup>2</sup> plot as seen in the older plots in this study is comparable with the richness in 200-m<sup>2</sup> plots found in many forest ecosystems in the world (see, e.g., Figure 17.1 in Fenton et al., 2015) while European heathlands, with only a few species, seem to be species-poor in comparison (Maltby et al., 1990).

Problems with using chronosequences in studies of successional patterns and processes are often discussed (Foster & Tilman, 2000), but in most cases they are used because it is the only option (Makoto & Wilson, 2019). Potential biases include major changes in climate or land use over the studied time period

(Pickett, 1989). We know from studies of satellite imagery and interviews that this area has had a similar land use system with traditional patch burning and grazing for many decades, even if the fire frequencies have increased somewhat, and fire sizes decreased in this study area over the last 40 years (Johansson et al., 2019). The good replication across time since fire and different burnt stands suggests that this chronosequence is a good example of a space-for-time approach with little risk for biases (Pickett, 1989).

### 4.3 | Bryophyte dispersal and succession

Anthropogenic fire regimes are characterized by more early-season, low-intensity and small-scale fires than natural fire regimes (Archibald et al., 2013). This typically creates a more fine-grained landscape mosaic, which facilitates species dispersal and speeds up recolonization. If neither adult individuals nor their propagules survive the disturbance, recolonization and succession are totally reliant on external propagule sources, sometimes called the external memory (Bengtsson et al., 2003; Mittelbach & Schemske, 2015). This seems to be the case in the burnt patches of heathland studied by us. Yet, it is also apparent that a large number of species are effective in colonizing the sites in a rather short time. The scientific community does not agree on the extent to which bryophytes and other organisms with small propagules (e.g., fungi and lichens) are dispersal-limited or not (Pharo & Zartman, 2007; Gjerde et al., 2014). One simple reason for this inconsistency might be that there is a large variability both between species in their dispersal capacity and between ecosystems in the likelihood that a propagule will establish (Barbé et al., 2016; Vanderpoorten et al., 2019). It is also important to be aware of the differences in both temporal and spatial scales when comparing results from different studies. A large proportion of the species observed in our study are fertile and produced sporophytes. The frequency of sporophytes is shown to be more important than for example terminal velocity (determined by spore size) in explaining colonization frequency in some systems (Lönnell & Hylander, 2018; Karlsson Tiselius et al., 2019). Studies show that spore-dispersed organisms can colonize sites hundreds or thousands of kilometres away if there is enough time (i.e. rare events that accumulate; Munoz et al., 2004; Désamoré et al., 2016). However, some studies suggest effective dispersal and colonization in few years over at least tens of kilometres (Lönnell et al., 2014; Lönnell & Hylander, 2018). This suggests that the spatial scale of the fires in this landscape (1–100 ha) is within the dispersal capacity of most of the spore-dispersed species and that changes in spatial configuration and fire size probably will not affect the bryophyte diversity or successional pathways much (but see Löbel et al., 2006; Zartman & Nascimento, 2006). Still, the decrease in the proportion of species with sporophytes along the successional gradient is in line with life-history theory proposing that some species utilize early successional stages with less competition by being fast colonizers, while other species are





slower colonizers, but better competitors (Huston & Smith, 1987; Chang & Turner, 2019).

#### 4.4 | The ecological role of *Breutelia* cover

Ecosystems in which bryophytes play a crucial role in fire dynamics are often characterized by a thick dense mat of a few moss species on the ground in later successional stages (Schimmel & Granström, 1997). This is also true in this system in which the cover of the acrocarpous moss *Breutelia diffracta* increases monotonically over time and builds up fluffy mats covering 15–45% of the ground 15 years after fire. Trampling by cattle likely reduces cover, but it is not known if a critical threshold of cover has to be reached for the moss to effectively carry the fire across the stand. However, from other studies in the same system it is known that sites less than five years after fire that on average have 10% cover of large mosses cannot burn (Johansson & Granström, 2014). Interestingly, it is also shown that the oldest stands burn less effectively, since there is a vertical separation between the moss layer and the canopy of the *Erica* shrubs (Johansson & Granström, 2014).

#### 4.5 | Implications for conservation management in a changing world

To develop sustainable conservation strategies, we need an understanding of the temporal dynamics of ecosystems over longer time scales. This is true for ecosystems with little direct impact from humans as well as for cultural landscapes in which the biodiversity is tightly connected with land use practices. The East African Afroalpine heathlands is a cultural landscape with a long history of traditional fire and grazing management (Johansson et al., 2012). However, these landscapes also provide habitats for species that also occur in less intensely managed systems, such as the Afroalpine as well as in the sub-alpine forest environments that border onto the heathlands above and below. Recently we demonstrated that the traditional land use of the heathlands allows high-altitude plants to grow at lower altitudes, thus potentially increasing the resilience of this unique flora in the face of climate change (Johansson et al., 2018). We know too little about the bryophyte flora and its spatial distribution to be able to explore this question with this data set. However, it is likely that also for this group of species, traditional fire and grazing management contribute to the rich biodiversity, potentially including species with optima at higher altitudes that benefit from decreased competition. There is a need to investigate the dynamics of all kinds of organisms in an ecosystem, to get a more holistic picture of possible outcomes of management policy (Van Mantgem et al., 2015; Bhaskar et al., 2019; Pilon et al., 2020). Fire is often regarded as destructive, even when it has shaped the ecosystem for a long time. On top of that, there is a pressure for increasing carbon

storage to mitigate climate change (Veldman et al., 2015). However, there is a risk of forgetting the important role of anthropogenic fire in the maintenance of a rich biodiversity (He et al., 2019). Despite the apparent lack of special adaptations to fire, it appears that the current fire and grazing regime in these heathlands is promoting and maintaining a rich bryophyte flora in a system where the bryophytes are a main regulator of the fire return interval.

#### ACKNOWLEDGEMENTS

We thank Ayano Abraham for invaluable field assistance, and Philip Sollman, John Spence, and Sven Fransson for help with the identification of difficult taxa. Funding was provided by Formas (Grant No. 231-2013-1973 to MUJ) and SIDA (Minor Field Study to CAF).

#### AUTHOR CONTRIBUTIONS

MUJ, CAF and KH conceived the ideas and designed methodology; CAF collected the data; SN gave advice in the field; KH identified the species, analyzed the data, wrote the first draft of the manuscript and led the writing. All authors contributed to the writing and interpretation of the results, and gave final approval for publication.

#### DATA AVAILABILITY STATEMENT

All data are available at DRYAD <https://doi.org/10.5061/dryad.866t1g1q9>.

#### ORCID

Kristoffer Hylander  <https://orcid.org/0000-0002-1215-2648>

Maria Ulrika Johansson  <https://orcid.org/0000-0001-8032-6075>

#### REFERENCES

- Archibald, S., Lehmann, C.E.R., Gomez-Dans, J.L. & Bradstock, R.A. (2013) Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 6442–6447. <https://doi.org/10.1073/pnas.1211466110>
- Barbé, M., Fenton, N.J. & Bergeron, Y. (2016) So close and yet so far away: long-distance dispersal events govern bryophyte metacommunity reassembly. *Journal of Ecology*, 104, 1707–1719. <https://doi.org/10.1111/1365-2745.12637>
- Bengtsson, J., Angelstam, P., Elmquist, T., Emanuelsson, U., Folke, C., Ihse, M. et al (2003) Reserves, resilience and dynamic landscapes. *AMBIO: A Journal of the Human Environment*, 32, 389–396. <https://doi.org/10.1579/0044-7447-32.6.389>
- Bhaskar, D., Easa, P.S., Sreejith, K.A., Skejo, J. & Hochkirch, A. (2019) Large scale burning for a threatened ungulate in a biodiversity hotspot is detrimental for grasshoppers (Orthoptera: Caelifera). *Biodiversity and Conservation*, 28, 3221–3237. <https://doi.org/10.1007/s10531-019-01816-6>
- Bird, R.B., Bird, D.W., Codding, B.F., Parker, C.H. & Jones, J.H. (2008) The “fire stick farming” hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proceedings of the National Academy of Sciences*, 105, 14796–14801. <https://doi.org/10.1073/pnas.0804757105>

- Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, 20, 387–394. <https://doi.org/10.1016/j.tree.2005.04.025>
- Bond-Lamberty, B., Peckham, S.D., Ahl, D.E. & Gower, S.T. (2007) Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature*, 450, 89–92. <https://doi.org/10.1038/nature06272>
- Chang, C.C. & Turner, B.L. (2019) Ecological succession in a changing world. *Journal of Ecology*, 107, 503–509. <https://doi.org/10.1111/1365-2745.13132>
- Désamoré, A., Patiño, J., Mardulyn, P., Mcdaniel, S.F., Zanatta, F., Laenen, B. & et al (2016) High migration rates shape the postglacial history of amphi-Atlantic bryophytes. *Molecular Ecology*, 25, 5568–5584. <https://doi.org/10.1111/mec.13839>
- During, H.J. (1979) Life strategies of Bryophytes: a preliminary review. *Lindbergia*, 5, 2–18.
- Esposito, A., Mazzoleni, S. & Strumia, S. (1999) Post-fire bryophyte dynamics in Mediterranean vegetation. *Journal of Vegetation Science*, 10, 261–268. <https://doi.org/10.2307/3237147>
- Fenton, N.J. & Bergeron, Y. (2008) Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal *Picea mariana* forests. *Biological Conservation*, 141, 1389–1399. <https://doi.org/10.1016/j.biocon.2008.03.019>
- Fenton, N.J. & Bergeron, Y. (2013) Stochastic processes dominate during boreal bryophyte community assembly. *Ecology*, 94, 1993–2006. <https://doi.org/10.1890/12-1944.1>
- Fenton, N., Hylander, K. & Pharo, E. (2015) Bryophytes in forest ecosystems. In Peh, K.S.H., Bergeron, Y. & Corlett, R.T. (Ed.) *Handbook in forest ecology*. London, New York: Routledge, pp. 239–249.
- Foster, B.L. & Tilman, D. (2000) Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecology*, 146, 1–10. <https://doi.org/10.1023/A:1009895103017>
- Friis, I. (1986) Zonation of forest vegetation on the south slope of Bale Mountains, South Ethiopia. *Sinet*, 9, 29–44.
- Gil-Romera, G., Adolf, C., Benito, B.M., Bittner, L., Johansson, M.U., Grady, D.A. et al (2019) Long-term fire resilience of the Ericaceous Belt, Bale Mountains, Ethiopia. *Biology Letters*, 15(7), 20190357. <https://doi.org/10.1098/rsbl.2019.0357>
- Gjerde, I., Blom, H.H., Heegaard, E. & Sætersdal, M. (2014) Lichen colonization patterns show minor effects of dispersal distance at landscape scale. *Ecography*, 38, 939–948. <https://doi.org/10.1111/ecog.01047>
- Gustafsson, J. (2009) *Habitat and plant selection of livestock in a fire-managed Afro-alpine heathland in Ethiopia*. SLU, Institutionen för skogens ekologi och skötsel, Umeå, Sweden.
- He, T., Lamont, B.B. & Pausas, J.G. (2019) Fire as a key driver of Earth's biodiversity. *Biological Reviews*, 94(6), 1983–2010. <https://doi.org/10.1111/brv.12544>
- Hedberg, O. (1964) Features of afroalpine plant ecology. *Acta Phytogeographica Suecica*, 49, 1–144.
- Huston, M. & Smith, T. (1987) Plant succession – life-history and competition. *The American Naturalist*, 130, 168–198. <https://doi.org/10.1086/284704>
- Hutsemékers, V., Dopagne, C. & Vanderpoorten, A. (2008) How far and how fast do bryophytes travel at the landscape scale? *Diversity and Distributions*, 14, 483–492. <https://doi.org/10.1111/j.1472-4642.2007.00454.x>
- Hylander, K. (2009) No increase in colonization rate of boreal bryophytes close to propagule sources. *Ecology*, 90, 160–169. <https://doi.org/10.1890/08-0042.1>
- Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J.R., Stillwell, M. & Zinnel, K.C. (1987) Old-field succession on a Minnesota sand plain. *Ecology*, 68, 12–26. <https://doi.org/10.2307/1938801>
- Jean, M., Alexander, H.D., Mack, M.C. & Johnstone, J.F. (2017) Patterns of bryophyte succession in a 160-year chronosequence in deciduous and coniferous forests of boreal Alaska. *Canadian Journal of Forest Research*, 47, 1021–1032. <https://doi.org/10.1139/cjfr-2017-0013>
- Johansen, J.R. (2001) Impacts of fire on biological soil crusts. In: Belnap, J. & Lange, O.L. (Eds.) *Biological soil crusts: structure, function, and management*. Berlin, Heidelberg, Germany: Springer, pp. 385–397.
- Johansson, M.U., Fetene, M., Malmer, A. & Granström, A. (2012) Tending for cattle: traditional fire management in Ethiopian montane heathlands. *Ecology and Society*, 17, 136–150. <https://doi.org/10.5751/ES-04881-170319>
- Johansson, M.U., Frisk, C.A., Nemomissa, S. & Hylander, K. (2018) Disturbance from traditional fire management in subalpine heathlands increases Afro-alpine plant resilience to climate change. *Global Change Biology*, 24, 2952–2964. <https://doi.org/10.1111/gcb.14121>
- Johansson, M.U. & Granström, A. (2014) Fuel, fire and cattle in African highlands: traditional management maintains a mosaic heathland landscape. *Journal of Applied Ecology*, 51, 1396–1405. <https://doi.org/10.1111/1365-2664.12291>
- Johansson, M., Senay, S., Creathorn, E., Kassa, H. & Hylander, K. (2019) Change in heathland fire sizes inside vs. outside the Bale Mountains National Park, Ethiopia, over 50 years of fire-exclusion policy: lessons for REDD+. *Ecology and Society*, 24(4). <https://doi.org/10.5751/ES-11260-240426>
- Karlsson Tiselius, A., Lundbäck, S., Lönnell, N., Jansson, R. & Dynesius, M. (2019) Bryophyte community assembly on young land uplift islands – Dispersal and habitat filtering assessed using species traits. *Journal of Biogeography*, 10, 2188–2202. <https://doi.org/10.1111/jbi.13652>
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G. & Rundel, P.W. (2012) *Fire in Mediterranean ecosystems: ecology, evolution and management*. Cambridge: Cambridge University Press.
- Keeley, J.E. & Fotheringham, C.J. (2003) Plot shape effects on plant species diversity measurements. *Journal of Vegetation Science*, 16, 249–256. <https://doi.org/10.1111/j.1654-1103.2005.tb02362.x>
- Keeley, J.E., Fotheringham, C.J. & Baer-Keeley, M. (2005) Factors affecting plant diversity during post-fire recovery and succession of Mediterranean-climate shrublands in California, USA. *Diversity and Distributions*, 11, 525–537. <https://doi.org/10.1111/j.1366-9516.2005.00200.x>
- Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16, 406–411. <https://doi.org/10.1016/j.tplants.2011.04.002>
- Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A. et al (2014) Savanna vegetation-fire-climate relationships differ among continents. *Science*, 343, 548–552. <https://doi.org/10.1126/science.1247355>
- Löbel, S., Snäll, T. & Rydin, H. (2006) Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. *Journal of Ecology*, 94, 856–868. <https://doi.org/10.1111/j.1365-2745.2006.01114.x>
- Lönnell, N. & Hylander, K. (2018) Calcicolous plants colonize limed mires after long-distance dispersal. *Journal of Biogeography*, 45, 885–894. <https://doi.org/10.1111/jbi.13180>
- Lönnell, N., Jonsson, B.G. & Hylander, K. (2014) Production of diaspores at the landscape level regulates local colonization: an experiment with a spore-dispersed moss. *Ecography*, 37, 591–598. <https://doi.org/10.1111/j.1600-0587.2013.00530.x>
- Magill, R.E. (1987) *Flora of Southern Africa*. Bryophyta, Part 1: Mosses. Botanical Research Institute, Pretoria.
- Makoto, K. & Wilson, S.D. (2019) When and where does dispersal limitation matter in primary succession? *Journal of Ecology*, 107, 559–565. <https://doi.org/10.1111/1365-2745.12988>
- Mallik, A.U. (1995) Conversion of temperate forests into heaths: role of ecosystem disturbance and ericaceous plants. *Environmental Management*, 19(5), 675–684. <https://doi.org/10.1007/BF02471950>
- Maltby, E., Legg, C.J. & Proctor, M.C.F. (1990) The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation. *Journal of Ecology*, 78, 490–518. <https://doi.org/10.2307/2261126>



- Miehe, G. & Miehe, S. (1993) On the physiognomic and floristic differentiation of ericaceous vegetation in the Bale Mountains, SE Ethiopia. *Opera Botanica*, 121, 85–112.
- Miehe, G. & Miehe, S. (1994) Bryophytes from the Bale Mountains, S.E. Ethiopia. 1 Phyto-ecological Introduction. *Fragmenta Floristica et Geobotanica*, 39, 165–219.
- Mittelbach, G.G. & Schemske, D.W. (2015) Ecological and evolutionary perspectives on community assembly. *Trends in Ecology and Evolution*, 30, 241–247. <https://doi.org/10.1016/j.tree.2015.02.008>
- Munoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R. & Martínez, I. (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science*, 304, 1144–1147. <https://doi.org/10.1126/science.1095210>
- O'Shea, B.J. (2006) Checklist of the mosses of sub-Saharan Africa (version 3, 11/99). *Tropical Bryology Research Reports*, 5, 1–252. [http://www.nhm.ac.uk/hosted\\_sites/bbstbg/resources\\_lit\\_africa.html](http://www.nhm.ac.uk/hosted_sites/bbstbg/resources_lit_africa.html)
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al (2019) *vegan: Community Ecology Package*. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>
- Perold, S.M. (1999) *Flora of South Africa. Hepatophyta, Part 1: Marchantiopsida*. National Botanical Institute, Pretoria.
- Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A. et al (2019) Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, 568, 88–92. <https://doi.org/10.1038/s41586-019-1048-z>
- Pharo, E.J., Meagher, D.A. & Lindenmayer, D.B. (2013) Bryophyte persistence following major fire in Eucalypt forest of southern Australia. *Forest Ecology and Management*, 296, 24–32. <https://doi.org/10.1016/j.foreco.2013.01.018>
- Pharo, E. & Zartman, C.E. (2007) Bryophytes in a changing landscape: the hierarchical effects of habitat fragmentation on ecological and evolutionary processes. *Biological Conservation*, 135, 315–325. <https://doi.org/10.1016/j.biocon.2006.10.016>
- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.) *Long-term Studies in Ecology*. New York: Springer, pp. 110–135.
- Pilon, N.A., Cava, M.G.B., Hoffmann, W.A., Abreu, R.C.R., Fidelis, A. & Durigan, G. (2020) The diversity of post-fire regeneration strategies in the Cerrado ground layer. *Journal of Ecology*, 109(1), 154–166. <https://doi.org/10.1111/1365-2745.13456>
- R Core Team (2019) *R 3.6.1: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria: the R Foundation for Statistical Computing.
- Rees, D.C. & Juday, G.P. (2002) Plant species diversity on logged versus burnt sites in central Alaska. *Forest Ecology and Management*, 155, 291–302. [https://doi.org/10.1016/S0378-1127\(01\)00566-7](https://doi.org/10.1016/S0378-1127(01)00566-7)
- Riccardi, C.L., Ottmar, R.D., Sandberg, D.V., Andreu, A., Elman, E., Kopper, K. et al (2007) The fuelbed: a key element of the Fuel Characteristic Classification System. *Canadian Journal of Forest Research*, 37, 2394–2412. <https://doi.org/10.1139/X07-143>
- Ryömä, R. & Laaka-Lindberg, S. (2005) Bryophyte recolonization on burnt soil and logs. *Scandinavian Journal of Forest Research*, 20, 5–16. <https://doi.org/10.1080/14004080510043361>
- Schimmel, J. & Granström, A. (1997) Fuel succession and fire behavior in the Swedish boreal forest. *Canadian Journal of Forest Research*, 27, 1207–1216. <https://doi.org/10.1139/x97-072>
- Schuler, L., Hemp, A., Zech, W. & Behling, H. (2012) Vegetation, climate and fire-dynamics in East Africa inferred from the Maundi crater pollen record from Mt Kilimanjaro during the last glacial-interglacial cycle. *Quaternary Science Reviews*, 39, 1–13. <https://doi.org/10.1016/j.quascirev.2012.02.003>
- Smith, R.J., Abella, S.R. & Stark, L.R. (2014) Post-fire recovery of desert bryophyte communities: effects of fires and propagule soil banks. *Journal of Vegetation Science*, 25, 447–456. <https://doi.org/10.1111/jvs.12094>
- Spehn, E.M. (2006) *Land use change and mountain biodiversity*. Boca Raton, FL: CRC Press.
- Tucker, C.M. & Cadotte, M.W. (2013) Fire variability, as well as frequency, can explain coexistence between seeder and resprouter life histories. *Journal of Applied Ecology*, 50, 594–602. <https://doi.org/10.1111/1365-2664.12073>
- Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Froliking, S., McGuire, A.D. & et al (2012) The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, 196, 49–67. <https://doi.org/10.1111/j.1469-8137.2012.04254.x>
- Van Mantgem, E.F., Keeley, J.E. & Witter, M. (2015) Faunal responses to fire in Chaparral and Sage scrub in California, USA. *Fire Ecology*, 11, 128–148. <https://doi.org/10.4996/fireecology.1103128>
- Vanderpoorten, A., Patiño, J., Désamoré, A., Laenen, B., Górski, P., Papp, B. et al (2019) To what extent are bryophytes efficient dispersers? *Journal of Ecology*, 107, 2149–2154. <https://doi.org/10.1111/1365-2745.13161>
- Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Wilson Fernandes, G. et al (2015) Where tree planting and forest expansion are bad for biodiversity and ecosystem services. *BioScience*, 65, 1011–1018. <https://doi.org/10.1093/biosci/biv118>
- Waters, M.T., Smith, S.M. & Nelson, D.C. (2011) Smoke signals and seed dormancy. *Plant Signaling and Behavior*, 6, 1418–1422. <https://doi.org/10.4161/psb.6.9.17303>
- Wesche, K., Miehe, G. & Kaeppeli, M. (2000) The significance of fire for Afroalpine ericaceous vegetation. *Mountain Research and Development*, 20, 340–347.
- Wigginton, M.J. (2009) Checklist and distribution of the liverworts and hornworts of sub-Saharan Africa, including the East African Islands (edition 3). *Tropical Bryology Research Reports*, 8, 1–116.
- Wills, A.J., Cranfield, R.J., Ward, B.G. & Tunsell, V.L. (2018) Cryptogam recolonization after wildfire: leaders and laggards in assemblages? *Fire Ecology*, 14, 65–84. <https://doi.org/10.4996/fireecology.140165084>
- Zartman, C.E. & Nascimento, E.M. (2006) Are habitat-tracking meta-communities dispersal limited? Inferences from abundance-occupancy patterns of epiphylls in Amazonian forest fragments. *Biological Conservation*, 127, 46–54. <https://doi.org/10.1016/j.biocon.2005.07.012>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** Supplementary figures and tables to the results section

**Appendix S2.** Species list

**How to cite this article:** Hylander K, Frisk CA, Nemomissa S, Johansson MU. Rapid post-fire re-assembly of species-rich bryophyte communities in Afroalpine heathlands. *J Veg Sci*. 2021;32:e13033. <https://doi.org/10.1111/jvs.13033>