CSIRO PUBLISHING

International Journal of Wildland Fire **2020**, *29*, 530–540
https://doi.org/10.1071/WF19106

Post-wildfire moss colonisation and soil functional enhancement in forests of the southwestern USA

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Abstract. Fire mosses, including *Ceratodon purpureus*, *Funaria hygrometrica* and *Bryum argenteum*, can achieve high cover within months to years after high-severity fire, but do so heterogeneously across space and time. We conducted a survey of moss cover and erosion-related functions after 10 wildfires in *Pinus ponderosa* and mixed-conifer forests of the southwestern USA. We sampled 65 plots in high-severity patches, stratifying by elevation and insolation over each fire. Using three landscape-scale predictor variables and one temporal predictor, we explained 37% of the variance in fire moss cover using a random forest model. The predictors in order of importance were: equinox insolation (sunlight/day), pre-fire vegetation type, pre-fire soil organic carbon and time since fire. Within each plot we examined differences between bare and moss-covered soil surface microsites and found moss-covered microsites had a mean increase of 55% water infiltration, 106% shear strength, 162% compressive strength and 195% aggregate stability. We tested a suite of nutrients, finding 35% less manganese in the moss-covered soil. This research demonstrated that post-fire colonisation by moss is predictable and that colonisation improves soil surface erosion resistance and hydrological function, with implications for managing severely burned landscapes.

Additional keywords: *Bryum argenteum*, *Ceratodon purpureus*, *Funaria hygrometrica*, mixed-conifer forest, ponderosa pine forest, post fire, soil erosion.

Received 12 July 2019, accepted 24 December 2019, published online 19 February 2020

Introduction

Fire extent and severity have been increasing in the southwestern USA due to climate change and elevated fuel densities (Keane *et al.* 2008; Abatzoglou and Williams 2016; Singleton *et al.* 2019). This creates an urgent need to better understand and adapt to the severely burned environment as it is quickly becoming a common landscape feature (Schoennagel *et al.* 2017). To assist land managers in understanding the severely burned environment, researchers have studied natural post-fire recovery of vascular plants in detail (Savage and Mast 2005; Kuenzi *et al.* 2008; Roccaforte *et al.* 2012; Owen *et al.* 2017). Non-vascular plants can be important post-fire colonisers as well. The recolonisation of the soil surface by the early successional mosses, *Ceratodon purpureus* (Hedw.) Brid. (Redshank), *Funaria hygrometrica* Hedw. (Cord moss), and *Bryum argenteum* Hedw. (Silvergreen moss), collectively known as fire mosses, has not been studied in the southwestern USA and only sparingly elsewhere (Hoffman 1966; Southorn 1977; Brasell and Mattay 1984; Hilty *et al.* 2004). These globally distributed species can achieve high cover in recently burned environments (Brasell and Mattay 1984).

Mosses have many functional traits that allow them to enhance ecosystem recovery after disturbances. For example, they have been documented to increase infiltration, aggregate soil surfaces and reduce erosion (Chamizo *et al.* 2012; Bu *et al.* 2015; Seitz *et al.* 2017; Silva *et al.* 2019). Fire mosses have both long- and short-distance dispersal methods, allowing them to quickly colonise and attain high cover in large severely burned patches (McDaniel and Shaw 2005; Ryömä and Laaka-Lindberg 2005; Jones and Rosentreter 2006; Frey and Kürschner 2011). Fire mosses, like other biocrusts, grow in a thin layer at the soil surface, stabilising soil to a degree disproportionate to their biomass (Jones *et al.* 1997). Fire mosses are desiccation tolerant, meaning they can dry without dying, allowing them to survive long periods of drought (Proctor *et al.* 2007). To our knowledge, no studies have focused on the natural role of mosses in post-fire recovery in the southwestern USA. Therefore, we conducted a survey of natural moss colonisation and function in recent high-severity burn patches in conifer forests with two main objectives. First, understanding the temporal- and landscape-scale drivers of moss cover will assist managers in predicting when and where fire moss could colonise. Second, exploring the moss-associated

Table 1. Fires sampled

TSF, time in decimal years between fire start date and sampling; moss cover, mean and (range) of moss cover plots within fire; AZ, Arizona; NM, New Mexico

Fire	Region	Start date	TSF (years)	Size (ha)	Plots	Moss cover (%)
Schultz	Flagstaff, AZ	20 June 2010	6.0, 7.0	5648	12	1.3 (0–10.1)
Slide	Flagstaff, AZ	20 June 2014	2.0, 3.0	8590	10	14.1 (0.6–46.1)
Camillo	Flagstaff, AZ	14 June 2015	2	9977	3	0.8 (0–2.35)
Pivot Rock	Flagstaff, AZ	18 May 2016	1.1	2434	4	0.02 (0.02–0.02)
Jack	Flagstaff, AZ	29 May 2016	0.22, 1.1	24 709	4	0 (0–0.025)
Las Conchas	Jemez Mountains, NM	26 June 2011	6	61 057	3	13.2 (3.2–22.0)
Thompson Ridge	Jemez Mountains, NM	31 May 2013	4	9186	4	22.7 (0.2–52.3)
Diego	Jemez Mountains, NM	25 June 2014	3.1	1467	3	5.7 (0–16.8)
Wallow	White Mountains, AZ	29 May 2011	5.1	228 107	15	14.6 (1–36.3)
San Juan	White Mountains, AZ	26 June 2014	2	2975	7	30.9 (1.4–72.9)

benefits in erosion resistance, hydrological function and soil nutrients will allow managers to better understand the potential value of preserving fire moss cover after wildfire.

We hypothesised that fire moss cover would reach its maximum within 2 years following fire, as documented in northwestern USA and Tasmania, Australia (Hoffman 1966; Brasell and Mattay 1984). To test this, we sampled fires at a range of elapsed times between fire and sampling (hereafter time since fire), from 2 months to 7 years. We hypothesised that mosses would prefer higher elevation sites on relatively shady hillslopes as seen in the northwestern USA (Hoffman 1966; Hilty *et al.* 2004; Durham *et al.* 2018). To test this, we selected plots that occurred in *P. ponderosa* and mixed-conifer forests at a range of elevations and winter solstice insolation positions (the amount of sunlight received on the winter solstice) within those ecosystem types, crossing factors to the maximum degree possible.

To test fire mosses' contribution to post-fire ecosystem erosion resistance and hydrological function, we compared bare mineral soil to moss-covered soil surfaces (hereafter bare versus moss) using a within-plot paired microsite technique. Biocrusts in Australian drylands have shown an affinity for trapping dust, so we hypothesised that moss would trap fugitive ash and its associated nutrients when compared with adjacent bare soils (Pereira *et al.* 2014; Mallen-Cooper and Eldridge 2016). Alternatively, mosses could preferentially uptake limiting nutrients and could decrease some nutrient concentrations. Because of mosses' ability to aggregate disturbed soil (Xiao *et al.* 2015; Seitz *et al.* 2017; Silva *et al.* 2019), we hypothesised fire moss would increase both erosion resistance and infiltration when compared with bare soil; we used four measurements to test this hypothesis.

Methods

Fire and plot selection

We selected three regions within the southwestern USA: Flagstaff in northern Arizona, the White Mountains in eastern Arizona and the Jemez Mountains in northern New Mexico. Each region experienced multiple severe fires in the recent past. Within these regions, we selected fires encompassing a range of times since fire (Table 1). During the summers of 2016 and 2017 we sampled a total of 10 fires.

Within each fire, we selected plots in high-severity burned areas as determined by Monitoring Trends in Burn Severity (MTBS). High severity was based on the relativised differenced normalised burn ratio (RdNBR), a vegetation burn severity index that is standardised for between-fire comparisons (Eidenshink *et al.* 2007). We used RdNBR pixels >643, a threshold specific to the southwestern USA (Singleton *et al.* 2019). If MTBS products had not yet been created, we used the high soil burn severity class created by Burned Area Emergency Response assessment teams (Hudak *et al.* 2004). Because soil burn severity and RdNBR can be poorly correlated (Safford *et al.* 2008), we validated high canopy-burn severity in the field by observing tree mortality of $>90\%$. We limited our scope of inference to high burn severity areas because of the increased runoff and erosion potential from that class (Shakesby and Doerr 2006; Scott *et al.* 2009). To reduce the possibility of sampling small patches of high burn severity, we cropped the perimeter of each patch by 30 m or one pixel, thus deleting any patch two pixels wide or less. We selected a subset of pixels 30–230 m from accessible roads to minimise time spent walking to plots.

The remaining severely burned areas within each fire were stratified by elevation and winter solstice insolation to maximise the environmental diversity of plots sampled. A 10-m digital elevation model (DEM) was used for all calculations in this stratification (Gesch 2007). We first excluded areas with slopes $>85\%$ for safety, then extracted elevation from the remaining pixels. To derive insolation, we calculated direct radiation modified by terrain and total diffuse radiation at each hour of the day, but excluded the minimal effects of sky view and changes in relative humidity and temperature throughout the day (Corripio 2003). To stratify by insolation and elevation we used cluster analysis, an analytical tool used to conduct stratified sampling of multivariate environmental data (Hargrove and Hoffman 2004). We applied the computationally efficient k-means algorithm from the *Stats* R Package (Hartigan and Wong 1979). The number of clusters (k) per fire was selected arbitrarily depending on its size, environmental diversity and if we had previously sampled a similar time since fire, resulting in 3–15 clusters per fire (Table 1). To capture the full range of environmental diversity within fires, we first selected plots at the extreme values of elevation and insolation, then one plot location was selected at random from within each cluster.

Table 2. Predictors used for modelling moss cover at the landscape scale
N/A, not applicable

Predictor	Resolution	Units	Mean	Median	Range
Time since fire	N/A	Years	1315.32	1129	79–2559
Elevation	10 m	m	2388.87	2397.1	1569.93–3005.86
Slope	10 m	Degrees	15.53	15.1	1.01–41.93
Topographic wetness	10 m	Unitless	5.99	5.82	4.02–11.20
Equinox insolation	10 m	MJ m^{-2}	22.94	23.95	14.51–27.49
Equinox insolation 0900 hours	10 m	MJ m^{-2}	0.94	0.95	0.33–1.38
Precipitation	800 m	mm	687.81	683.41	538.21–887.40
Pre-fire soil organic carbon	100 m	Percentage	24.34	25.6	13.7–32.9
pH	100 m	Unitless	6.15	6.2	5.60–6.60
Geologic map unit	Polygon	N/A	N/A	N/A	N/A
Pre-fire vegetation type	30 m	N/A	N/A	N/A	N/A

We relocated four plots by up to 100 m to target specific topographic conditions or to avoid disturbed areas such as roads. Plots consisted of two 20-m transects, 20 m apart, along two parallel contours. At three plots, topography did not allow for 20 m of continuous hillslope so transects were moved closer together. We took Global Positioning System coordinates at the four corners created by the transect end points and averaged points to obtain plot locations for Geographic Information Systems (GIS) analysis. Along each transect, we measured percent fire moss cover using a line intercept method with a resolution of 1.5 cm (Canfield 1941). If moss was not found on a transect, we used a 5-min timed search within 5 m of the transects to determine presence or absence, allowing us to distinguish true absence from low abundance.

Paired microsite measurements

To test fire mosses' contribution to erosion resistance and hydrological function we measured paired bare versus moss microsites and collected paired soil samples for laboratory analysis (Bowker *et al.* 2006). This only occurred if moss cover was high enough, defined as roughly 400 cm^2 of moss in at least six patches per plot within a 5 m buffer around the transects. Microsites were spaced 10 cm to 2 m apart and microsite pairs were dispersed throughout the plot to the degree that moss cover allowed. At each plot we measured: infiltration rates at three bare versus moss pairs using a Mini Disc Infiltrometer™ (Meter Environment, Pullman, WA, USA, Robichaud *et al.* 2008); soil shear strength at six pairs using a Torvane™ shear vane (Durham Geo-Enterprises, Mukilteo, WA, USA, Zimbone *et al.* 1996); soil compressive strength at six pairs using a handheld penetrometer (QA Supplies, Norfolk, VA, USA, Zimbone *et al.* 1996); and soil aggregate stability at 12 pairs using a soil aggregate stability test kit (Herrick *et al.* 2001). To ensure a uniform hydraulic connection between the infiltrometer and the soil surface, we drove a 5-cm diameter metal ring into the soil 3 cm deep and added a thin layer of sand until the soil or moss was entirely covered. The infiltrometer was then held in place inside the ring using a stand, without applying any downward pressure. Microsites for Torvane and penetrometer measurements were wetted to field capacity with a spray bottle before taking measurements. At $<$10% of microsites, the functional measurement observed was below the detection limit of the instrument, so we assumed function was half of the lowest measurement increment of that instrument. To the degree possible, we sampled plots when the soil surface was dry to increase consistency of moss cover measurements between plots and soil moisture between moss and bare microsites.

We received permission to collect soil samples from all burned areas except two (the Wallow and San Juan Fires). Soil sampling consisted of 5–10 subsamples, depending on the size and number of moss patches available, directly under live moss tissue to a depth of 1.5 cm, and on the bare mineral soil microsites to a depth of 1.5 cm. We removed moss fragments from the samples before analysis. In the laboratory, soil samples were sieved in a 2-mm sieve and analysed for pH, total carbon, total nitrogen, available phosphate and a suite of available cations and trace metals, following the Forest Inventory Analysis Protocol (Amacher *et al.* 2003). Complete methods are provided in Text S1 available as Supplementary Material to this paper.

Landscape predictors of fire moss cover

To elucidate landscape-scale drivers of fire moss cover, we selected variables with continuous coverage within our study system. We selected 11 candidate predictors in six broad categories: temporal, topographic, solar, climatic, vegetative and edaphic (Table 2). Our first predictor variable was time since fire (years). Topographic predictors of elevation (m) and slope (degrees) were extracted using the same 10-m resolution DEM as in the plot selection methods. Topographic wetness index (unitless) was calculated from the DEM using SAGA GIS (Conrad *et al.* 2015). Two solar predictors of insolation (MJ m^{-2}) were calculated as described in the plot selection section. We used insolation on the equinox summed over the entire day and at 0900 hours. Equinox insolation was found to be a superior predictor to winter solstice insolation because some locations receive no direct sunlight in steep terrain during winter. Equinox insolation at 0900 hours was used to differentiate slopes that receive morning versus evening sun, which is a potential driver of hydration period length during daylight. PRISM climate normals (1981–2010) of yearly precipitation (mm) at a resolution of 800 m were extracted (Daly *et al.* 2008). Edaphic variables of pre-fire soil organic carbon (percentage) and pH, at 0 cm depth, were extracted from Soil Grids at a resolution of 100 m (mapping accuracies pseudo $R^2 = 0.41$ and 0.68, respectively, Ramcharan *et al.* 2018). An edaphic variable of geologic map unit containing 10 categories was extracted from the State Geologic Map Compilation geodatabase (Horton *et al.* 2017). Categories were combined into five major classes, Alluvium, Andesite, Basalt, Sedimentary and Tuff, to reduce the risk of spurious results from many categories (Hastie *et al.* 2017). We used the pre-fire 2012 LANDFIRE existing vegetation type layer at a resolution of 30 m to determine vegetative effects on moss growth (Ryan and Opperman 2013). Our dataset contained three categories: Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland (hereafter mesic mixed-conifer), Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland (hereafter dry-mesic mixed-conifer), and Southern Rocky Mountain Ponderosa Pine Woodland (hereafter ponderosa pine).

Modelling moss cover

We modelled moss cover in R version 3.5.1 (R Core Team 2019) using the random forest machine learning algorithm (Breiman 2001) in the randomForest package (Liaw and Wiener 2002). We first created a random forest model with all candidate predictors to assess variable importance. Then we optimised the model using a variable selection technique and finally reran the optimised model using the selected predictor variables. Random forest is a nonparametric machine learning algorithm implemented by taking bootstrap samples of the data and fitting decision trees to each replicate. At each decision tree node, the variable that minimised regression error was selected from a random subset of predictors. We used the total number of predictors divided by three for each node predictor subset. Nodes were split until no further reduction in error was achieved. Observations not selected in the bootstrapping process, termed 'out of bag' (OOB), were used to compute the mean squared regression error for each tree. We then averaged the errors and took the square root to calculate the model root mean squared error (RMSE). Random forest variable importance results can be sensitive to changes in random seed if the number of trees grown is too small (Strobl *et al.* 2008). We ran models multiple times using different random seeds and looked for rank changes in permutational variable importance of predictors. We found variable importance rank stability for the most important variables to be 5000 trees per model and three predictors per node subset.

When using random forests, selecting the most important variables not only increases model interpretability and parsimony, it can also improve model performance (Evans *et al.* 2010). The two major reasons for this improvement are: only good predictors are selected during the node splitting phase of the algorithm (Hastie *et al.* 2017) and, as spurious variables are removed from the model, trees tend to have fewer nodes, thus decreasing the noise of each tree and increasing the signal to noise ratio of the forest (Evans *et al.* 2010). We used the VSURF package to implement a variable selection approach (Genuer *et al.* 2015). The VSURF package ranks predictor variable importance and then uses a stepwise forward approach to introduce variables into the model. Predictors are only added if the decrease in OOB error is greater than a threshold value of the average variation explained by adding permuted predictors (Genuer *et al.* 2015).

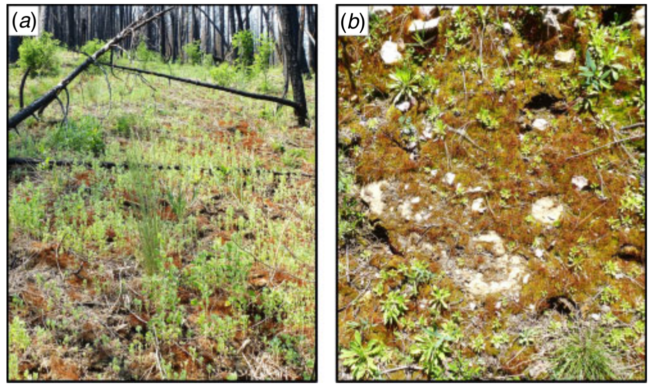

Fig. 1. High fire moss cover 2 years after fire: (*a*) 2014 San Juan Fire: and (*b*) 014 Slide Fire. Photo credit: Henry Grover.

After this selection technique we reran the randomForest package to create an optimised model using four predictor variables, with 500 trees, and one selected variable per node.

Visualising drivers of moss cover

Using the optimised model, we implemented a similar but improved version of partial dependence called Accumulated Local Effects (ALE) to create bivariate plots of how each predictor affected moss cover (Friedman 2001; Apley and Zhu 2019). ALE plots use a moving window to calculate how the predictor affects the response for data instances within that window. The advantage of ALE plots over partial dependence is their robustness when predictor variables are correlated (Apley and Zhu 2019). This technique was implemented using the IML package (Molnar *et al.* 2018). We included the raw data within each bivariate plot to increase interpretability.

Using the optimised model, we made a map of model-predicted moss cover and the three best predictors in severely burned conifer forests of the Slide Fire, 2 years post fire. One limitation to bivariate plots is that they do not allow us to visualise interactions between predictor variables. Interactions, however can be visualised on a map.

Paired microsite data

For each hydrologic and erosion measurement, at each microsite pair, we calculated the percent change from bare to moss-covered soil. We then calculated a plot level mean for each measurement type. Because soil samples were composited before analysis, plot level means of soil properties were measured directly. To calculate study-wide summary statistics of hydrologic and erosion measurements and soil nutrients we bootstrapped 95% confidence intervals for the mean with 10 000 replicates using the boot package (Canty 2002).

Results

Modelling moss cover

Moss cover ranged from 0% to 72.9% with a mean of 11.2% and a median of 3.5% (Fig. 1). Our initial model of moss cover had an OOB RMSE of 13.2 and a pseudo R^2 of 0.30. We used permutational variable importance, which is defined as the change in the model accuracy when that variable is permuted and the model rerun. It is robust to unstandardised predictor variable scales (Hastie *et al.* 2017). The most important variables were equinox insolation (57.1), pre-fire soil organic carbon (20.2) and precipitation (13.9, Fig. 2*a*). Time since fire, elevation and pre-fire vegetation type were the next most important variables. Their importance rank order changed with different random seeds and ranged from 12.0 to 11.6 (Fig. 2*a*). Equinox insolation at 0900 hours, geologic map unit, slope, topographic wetness index and pH were poor predictors of moss cover (Fig. 2*a*).

Four variables were selected for the optimised model: equinox insolation, pre-fire vegetation type, pre-fire soil carbon and time since fire. This model performed substantially better than the initial model with an OOB RMSE of 12.5 and a pseudo R^2 of 0.37. The most important predictor was equinox insolation (62.5), followed by pre-fire vegetation type (40.8), pre-fire soil organic carbon (31.5) and time since fire (20.1, Fig. 2*b*). The rank order importance of these predictors was consistent across six model runs with different random seeds.

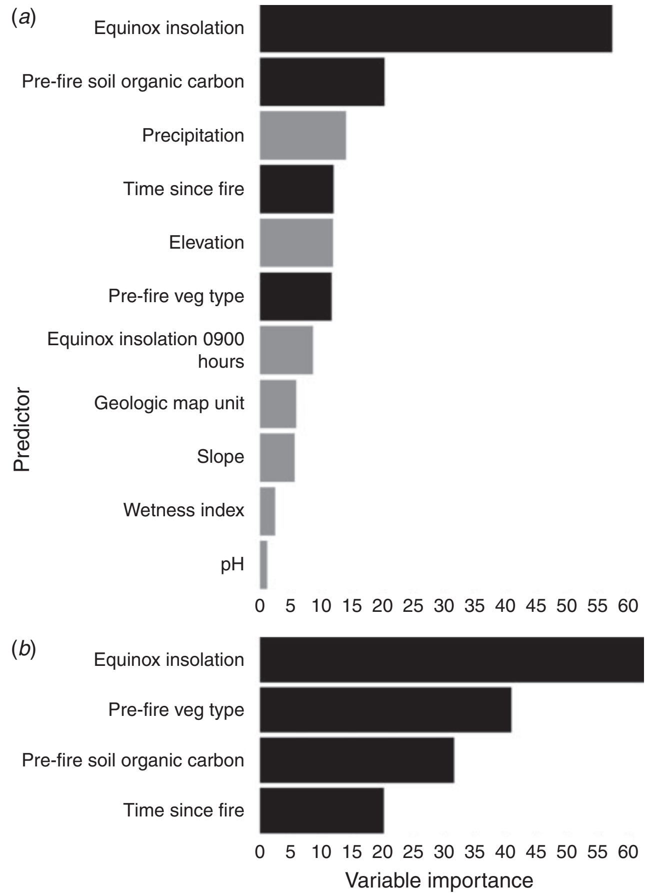

Fig. 2. Variable importance for (*a*) the *a priori* model, defined as the percent increase in root mean squared error (RMSE) when the variable of interest is permuted (RMSE = 13.2, pseudo $R^2 = 0.30$), and (*b*) variable importance scores for optimised model (RMSE = 12.5, pseudo $R^2 = 0.37$).

Visualising drivers of moss cover

In the ALE plots, moss cover had a relatively linear, inverse relationship with equinox insolation (Fig. 3*a*). Pre-fire vegetation type had three levels: moss cover was highest in mesic mixed-conifer forests with a mean of 17.0%, followed by ponderosa pine forests with a mean of 10.3%; dry-mesic mixed-conifer forests had the lowest moss cover at 6.9% (Fig. 3*b*). Moss cover was positively related to soil organic carbon with high moss cover found within a range of organic carbon values from 22% to 33% (Fig. 3*c*). Time since fire was the final predictor included in our optimised model. Initially, moss cover was low after fire but increased to a maximum at 2 years and then dissipated as time since fire increased to more than 5 years (Fig. 3*d*).

Predicted moss cover on the Slide Fire ranged from 0% to 44% and was heterogeneous across the landscape (Fig. 4*b*). Most of the area burned was south-facing with insolation levels above 20 MJ m^{-2} in the ponderosa pine ecosystem type (Fig. 4*b–c*). This resulted in <10% moss cover across most of the fire with localised patches of high cover in steeper north-facing slopes (Fig. 4*b–c*). This map was useful for visualising drivers of moss cover across the landscape; however, given our intermediate model performance metrics (RMSE = 12.5) and lack of independent cross-validation (Evans *et al.* 2010) we would expect differences between our predicted and actual cover values.

Paired microsite data

We examined nutrient differences on bare versus moss microsites at 29 plots in the Flagstaff and the Jemez Mountains. Only pH, potassium (K) and manganese (Mn) differed from bare to moss microsites (Fig. 5). We found that pH increased by 3.6% from a mean of 6.25 on bare to 6.45 on moss sites, K increased by 14.0% from a mean of 922.0 (mg kg^{-1} soil) on bare to 984.1 (mg kg^{-1}) on moss sites, and Mn concentrations decreased by 34.7% from bare to moss microsites.

Moss was superior to the bare soil surface for all metrics of erosion resistance and hydrological function (Fig. 6). Forty-eight plots had enough moss to measure infiltration and 50 had enough to measure shear strength compressive strength and aggregate stability. The percent difference from bare to moss microsites for each measurement were: percent change in infiltration ranged from −46% to 280.4% with a mean of 54.9% and a median of 48.2%; shear strength ranged from −30.1% to 645% with a mean of 105.9% and a median of 74.3%; compressive strength ranged from −23.7% to 578.6% with a mean of 162.2% and a median of 97.6%; and aggregate stability ranged from 0% to 500% with a mean of 195.2% and a median of 166.3%. None of the bootstrapped 95% confidence intervals for the mean overlapped zero (Fig. 6).

Discussion

Landscape-scale controls of fire mosses

Consistent with our hypothesis, moss colonisation negatively related to equinox insolation; that is, shady north-facing slopes had higher cover. The duration of continuous hydration, or conversely the speed of desiccation, often controls moss productivity (Proctor 1990; Proctor *et al.* 2007) and south-facing slopes in the northern hemisphere dry mosses more rapidly, limiting growth. This effect is amplified in severely burned

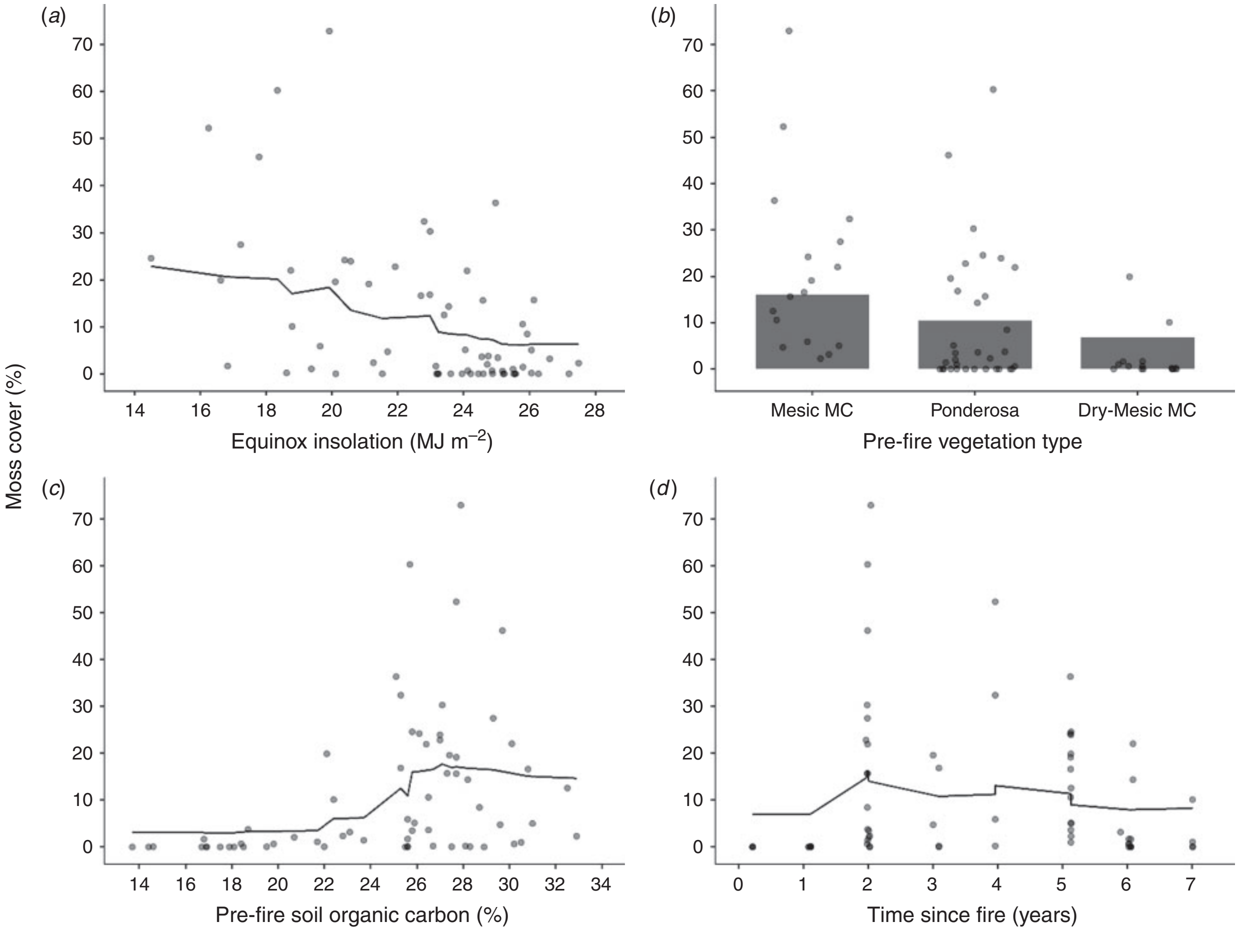

Fig. 3. Bivariate plots of predictors in the optimised model in order of importance: (*a*) equinox insolation, (*b*) pre-fire vegetation type (MC = mixed-conifer), (*c*) pre-fire soil surface organic carbon and (*d*) time since fire. Predictions (lines and bars) are random forest accumulated local effects, a visualisation of how each predictor variable affects the response when other main effects and interactions are accounted for. Points are plot values ($n = 65$). Black dots denote superimposed data points; in panel (*b*) points have been separated for easier visualisation.

forests where soil surface temperatures can be 3–7°C higher than in unburned forests (Montes-Helu *et al.* 2009). Conversely, mosses are relatively shade-tolerant with a median daily light saturation value across 39 species of 11 MJ m^{-2} (Marschall and Proctor 2004). The minimum equinox insolation value for our study was 14 MJ m^{-2}, so light limitation likely did not occur.

The importance of pre-fire vegetation type was not surprising, because it unites many different climatic and topographic factors into a single variable. Cooler and wetter regions supporting mesic mixed-conifer forests would be expected to enhance moisture retention time in surface soils and mosses, thus increasing growth. More puzzling was the finding of higher moss cover in ponderosa pine forests compared with dry-mesic mixed-conifer forests. This result was influenced by the fact that 10 of the 15 dry-mesic mixed-conifer plots sampled were within the Schultz Fire extent, which had among the lowest moss cover values (Table 1). We hypothesise that some feature of the Schultz Fire distinguishes it from the other fires in this study. For example, this fire experienced extremely high rates of post-fire erosion (Neary *et al.* 2012), which could have influenced subsequent moss growth. Alternatively, this fire was among the oldest sampled and it is plausible that our observations missed an earlier peak in biomass (Hoffman 1966; Brasell and Mattay 1984). To determine whether our observations are typical of dry-mesic mixed-conifer forests would require more intensive sampling of this community type.

Although it is true that vegetation types differ in surface soil organic carbon content with high values in mesic mixed-conifer forests, our results suggest there is predictive value in pre-fire soil organic carbon that is independent of vegetation type. The positive relationship between moss cover and pre-fire soil organic carbon could be attributed to an enhancement of the post-fire soil environment that enhances moss growth. While surveying, we often found within a given plot that fire mosses preferentially colonised soil adjacent to burned coarse woody debris (Ryömä and Laaka-Lindberg 2005). We hypothesise that a similar trend could be occurring at the landscape scale, wherein fire consumes soil carbon to create a substrate that is then preferentially colonised by moss. This hypothesis has been partially tested experimentally with fire mosses growing rapidly on unburned organic substrates in a greenhouse (Grover *et al.* 2019). However, fire mosses have

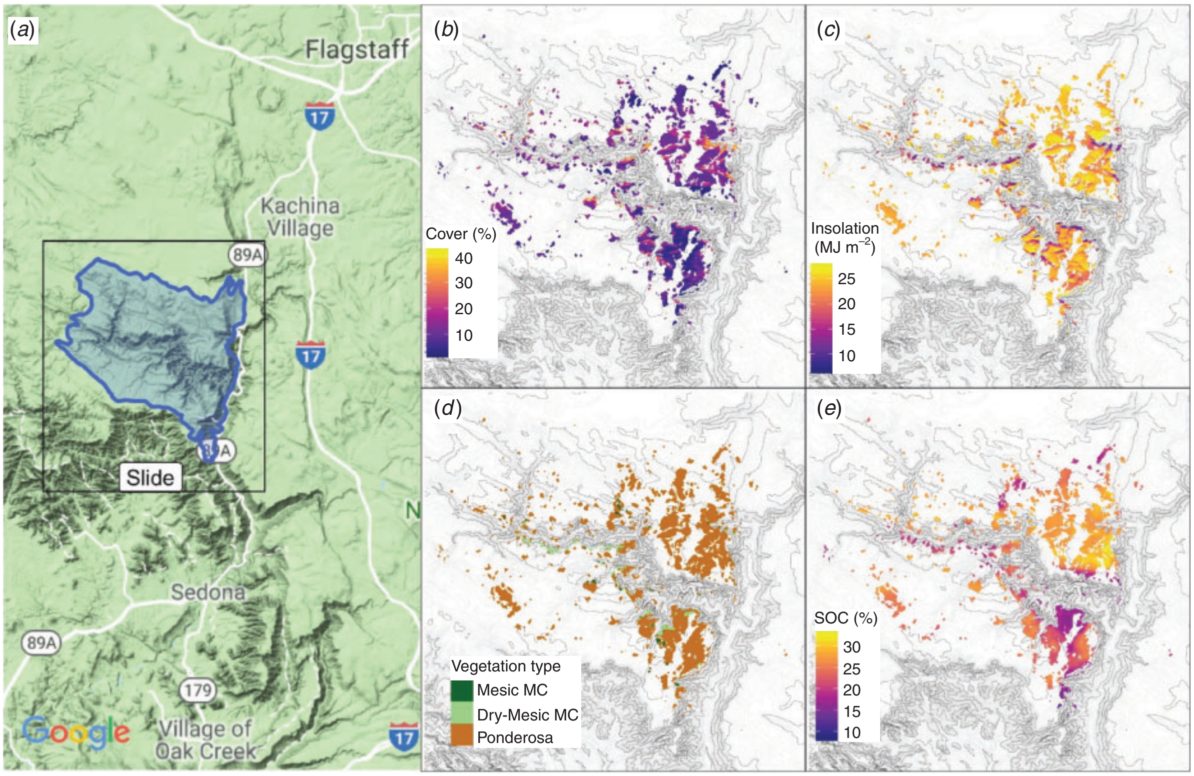

Fig. 4. A map of (*a*) the 2014 Slide Fire south of Flagstaff, AZ used for visualising interactions between the landscape scale predictor variables and their effect on fire moss cover. This map outlines (*b*) fire moss cover at 2 years after the fire, (*c*) equinox insolation, (*d*) pre-fire vegetation type (MC = mixed-conifer) and (*e*) pre-fire soil organic carbon (SOC).

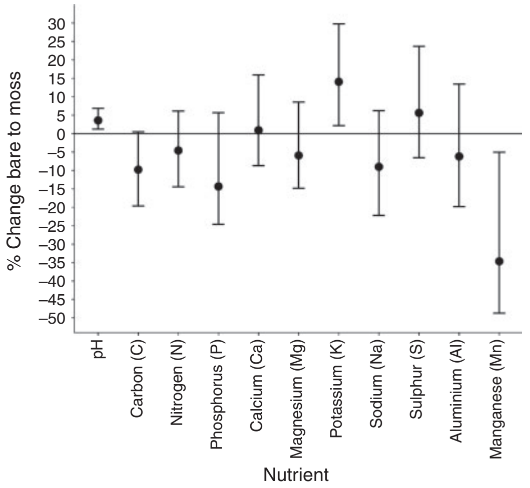

Fig. 5. Average percent change in pH and nutrient concentration from bare to moss-covered microsites. Error bars are bootstrapped 95% confidence intervals ($n = 31$).

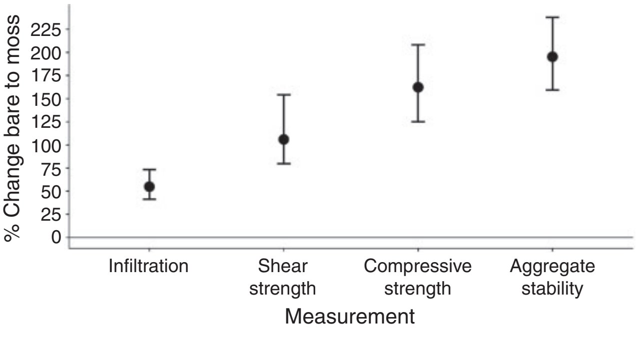

Fig. 6. Average percent change in hydrological function (infiltration) and erosion resistance (shear strength, compressive strength, aggregate stability) from bare to moss-covered microsites. Error bars are bootstrapped 95% confidence intervals. Infiltration ($n = 48$), shear strength, compressive strength and aggregate stability ($n = 50$).

also been shown to preferentially colonise bare mineral soil after disturbance (Gross 2009; Kranabetter *et al.* 2017).

The relationship between moss cover and time since fire is relatively noisy because of our within-fire plot stratification. However, there is support for our hypothesis that moss cover increases until 2 years post fire and gradually declines after that. This could be because of competition with vascular plants (Lewis *et al.* 2017) or changes in substrate as recovery occurs (Certini 2005), but we did not test this directly. The first 2 years post fire is a typical range of times in which maximum cover is seen in diverse ecosystems throughout the globe (Hoffman 1966; Brasell and Mattay 1984; Esposito *et al.* 1999; Silva *et al.* 2019). Our data seem to suggest an abrupt increase from very low cover to peak levels in year 2, but we have reason to suspect that our dataset may underestimate moss cover before 2 years post fire. During our sampling period of 2016 and 2017 there was a lack of predominantly high-severity wildfires in the southwestern USA. Instead, we sampled fires managed for ecosystem benefit that occurred in relatively flat topography, in ponderosa pine ecosystems, and did not create large patches of high burn severity. This is a limitation of the space-for-time substitution method. Early growth of mosses (<2 years post fire) merits further investigation with repeated monitoring of the same locations, beginning directly after wildfire within a diverse set of forest types.

The map of the 2014 Slide Fire shows the drivers of moss cover in complex terrain (Fig. 4). One can see the main effect of each variable, but the real utility of this map is examining how variables relate to each other. For example, we can see synergistic interactions on the eastern portion of the north rim of the canyon. Here, the convergence of low equinox insolation and high pre-fire soil organic carbon corresponds to patches of very high predicted moss cover. Conversely, we can see instances where some favourable conditions are met, but not others; for example on the eastern portion of the south rim of the canyon. There is a comparable amount of low equinox isolation habitat as on the north rim, but the patches of high predicted moss cover are fewer and smaller, possibly because the south rim of the canyon has a higher proportion of dry-mesic mixed-conifer forest than ponderosa pine forest, as well as lower pre-fire soil organic carbon. One relationship that is not easily visualised with this map is how elevational patterns could be driving pre-fire vegetation independently of equinox insolation (Merriam 1890). This pattern is evident in the San Juan and Wallow Fires because they spanned a wide range of elevations and equinox insolation. This contributes to the evidence that pre-fire vegetation type is a coarse but adequate predictor of elevation and climate.

Moss-mediated alterations of soil nutrients

High-severity fires affect soil nutrient concentrations and availability, with consequences for plants, especially at the soil surface (Certini 2005). With ash deposition, increases in pH and base cations are to be expected (Pereira *et al.* 2014). The increase in pH and K from bare to moss-covered microsites is consistent with scenarios in which mosses either preferentially colonise ash-covered soil or trap mobile ash, as dust is trapped by mosses in other environments (Mallen-Cooper and Eldridge 2016). The decrease in Mn under mosses could be attributed to moss depletion of Mn in the soil directly under it. Alternatively, Mn in mobile ash may be entrained in the moss cushion and physically prevented from entering the soil beneath.

Effect of moss on erosion resistance and infiltration

Flooding and erosion are among the costliest outcomes of high-severity fire; thus promoting biota that enhance ecosystem recovery is commonly a management priority. Our results show a doubling in erosion resistance on average and 1.5-fold more infiltration which point to the potential for mosses to reduce erosion and runoff after fire. It is generally accepted that a high surface cover of bare soil is a strong predictor of increased hillslope runoff and erosion (Scott *et al.* 2009). Our results indicate that fire moss cover could help remedy erosion and hydrological dysfunction and should be accounted for when considering post-fire management strategies.

Similar studies support our results that greater moss coverage leads to less erosion (Bu *et al.* 2015; Xiao *et al.* 2015; Seitz *et al.* 2017; Silva *et al.* 2019). Mosses may dissipate the force of falling raindrops or protect against the erosive force of runoff. A key caveat to our results is the point-scale at which these measurements were taken. Post-fire erosion is largely driven by the formation of rills and gullies which our experimental design did not take into account (Moody *et al.* 2013). Bu *et al.* (2015) tested point-scale soil shear strength measurements, which were predictive of erosion in 4×2 m runoff plots. Thus, our measurements likely scale up, but overall the literature is lacking data on the effect of mosses on erosion at hillslope and watershed scales.

Many of the same studies that support our finding of moss-enhanced erosion resistance did not find enhanced infiltration or reduced runoff on moss-covered soils (Bu *et al.* 2015; Xiao *et al.* 2015; Silva *et al.* 2019). This discrepancy is likely due to differences between tension infiltrometer and runoff plot methodology. Experimental manipulations focused on moss-covered burned soils reaction to both sheet flow and channelised flow would be useful to understand function at increased scales (Pannkuk and Robichaud 2003).

Conclusions

This research provides a better understanding of the distribution and potential limitations to growth of a previously understudied early successional post-fire community. We found that fire mosses generally prefer shady hillslopes in mesic forests with high pre-fire soil organic carbon and reach maximum cover 2 years post fire. Furthermore, we provide evidence that post-fire moss growth is likely to positively affect erosional and hydrological function. This moss-associated increase in function suggests that managers should actively encourage moss cover and avoid disturbances that potentially inhibit it after fire. This study creates a basis for testing the effects of post-fire management techniques such as Burned Area Emergency Response treatments or salvage logging on fire moss colonisation. The global distributions of fire mosses mean that they could be an important component of the post-fire community in other regions and ecosystems that experience high-severity fire and should continue to be studied both for their ecological significance and potential utility in post-fire rehabilitation.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

The authors thank Christopher MacDonald and Robert Parmenter for providing access and support with obtaining permits. Suzanne Owen and Steven Overby designed, and Danna Muise and Sedona Spann conducted the nutrient analysis. This work would not have been possible without the technicians and volunteers who provided field and laboratory support, including Channing Laturno, Daniel'le DeVoss, Kara Gibson, Dean Grover, Dustin Kebble, Landon Kuestersteffen, Pablo Ortiz, Carla Roybal, Sedona Spann and Michael Sloan. Finally, we wish to thank Peter Robichaud, Shannon Kay, Derek Sonderegger and two anonymous reviewers for input that greatly improved this manuscript. This work was supported by the McIntire-Stennis Cooperative Forestry Research Program (grant no. USDA-NIFA-10202-MSCFRXXX-19-001 / project accession no. 1007836) from the USDA National Institute of Food and Agriculture. Additional funding was provided by Valles Caldera National Preserve, Jemez, NM (Agreement ID: P16AC00911); the ARCS foundation scholar award, Phoenix, AZ; and the Joint Fire Science Program, Graduate Research Innovation (GRIN) award (Grant ID: 18-1-01-55). Field technician support and soil sample analysis were provided by the Rocky Mountain Research Station, Flagstaff, AZ.

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