

RESEARCH ARTICLE

Desiccation and rehydration of mosses greatly increases resource fluxes that alter soil carbon and nitrogen cycling

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Abstract

1. Mosses often have positive effects on soil carbon and nitrogen cycling, but we know little about how environmentally determined cycles of desiccation and rehydration in mosses influence these processes.
2. In this context, we compared carbon and nitrogen in throughfall after precipitation passed through eight moss species that were either hydrated continuously or desiccated and rehydrated. Also, the throughfall of four moss species was added to soil and used to determine the net effect of carbon and nitrogen added in moss throughfall on soil CO₂ and N₂O efflux.
3. Depending on the species, desiccated-rehydrated (rehydrated) mosses lost 2–31 times more carbon in throughfall than mosses that were continuously hydrated (hydrated). Hydrated mosses lost little to no detectable nitrogen, whereas most rehydrated mosses lost some nitrogen in throughfall. Throughfall from both hydrated and rehydrated mosses generated higher CO₂ and N₂O efflux than water treated soils, but rehydrated moss throughfall promoted larger N₂O efflux than hydrated moss throughfall. Throughfall from hydrated mosses caused net negative changes in soil carbon and had very little effect on soil nitrogen, whereas throughfall from rehydrated mosses generated positive changes in soil carbon and nitrogen.
4. *Synthesis.* Our results indicate that resources lost from desiccated mosses during rehydration influence soil carbon and nitrogen transformations and may be important drivers of carbon and nitrogen cycling and storage in ecosystems.

KEYWORDS

bryophyte, carbon storage and loss, ecosystem function, moss, nitrogen storage and loss, throughfall

1 | INTRODUCTION

Our understanding of how primary producers affect ecosystems is largely informed by vascular plants, but nonvascular plants like mosses also influence ecosystems. Like vascular plants, mosses modify their environment by buffering soil temperature and moisture, decreasing surface water runoff and enhancing soil water retention (Blok et al., 2011; Gornall, Jónsdóttir, Woodin, & Van der

Wal, 2007; Pócs, 1980; Veneklaas et al., 1990). Mosses and vascular plants both have a positive influence on soil organic matter, soil total carbon (C) and soil total nitrogen (N), which for mosses has been attributed to their direct effects on soil temperature and moisture (Gornall et al., 2007; Lamontagne, 1998; Sedia & Ehrenfeld, 2005; Sun et al., 2017; Turetsky, Mack, Hollingsworth, & Harden, 2010; Zhao, Li, Zhang, Hu, & Chen, 2014). Unlike vascular plants, the high cation-exchange and water holding capacity of moss tissue leads to

the substantial accumulation of nutrients from symbiotic nitrogen fixation, precipitation and forest canopy throughfall (Lagerström, Nilsson, Zackrisson, & Wardle, 2007; Street et al., 2013; Turetsky et al., 2010). Perhaps as important, and distinctly different from vascular plants, mosses are poikilohydrous. When water is not available, mosses desiccate, equilibrating their cellular water content with water levels of ambient air and often compromising their cellular integrity during the process. When mosses rehydrate, damaged cell membranes introduce openings through which intracellular contents (carbohydrates, inorganic nitrogen, amino acids and ionic compounds) are lost (Bach, Frostegård, & Ohlson, 2009; Carleton & Read, 1991; Coxson, 1991; Startsev & Lieffers, 2006; Wilson & Coxson, 1999). Mosses coordinate a suite of fine-tuned morphological, physiological and molecular strategies to survive these repeated cycles of drying and rewetting (Green, Sancho, & Pintado, 2011; Oliver, Velten, & Mishler, 2005) that are determined by their evolutionary history and short-term environmental history. Thus, these species and habitat-specific strategies employed by mosses to survive desiccation may generate differences in the quantity and quality of intracellular contents lost from mosses during rehydration. However, to date, our understanding of how mosses influence communities and ecosystems has not accounted for these 'bryotic' pulses of resources lost during moss rehydration. Quantifying bryotic pulses across moss species and habitats may provide insight into mechanisms by which mosses affect their environment and other plant species, and improve previous quantitative estimates of the overall effect of mosses on ecosystems.

Several studies have compared the leakiness of continuously hydrated (hydrated hereafter) mosses to that of desiccated-rehydrated (rehydrated) mosses in Petri dishes filled with water. In these studies, rehydrated mosses lost more intracellular C, N and potassium (K) into the water than hydrated mosses due to cellular membrane damage (Brown & Buck, 1979; Carleton & Read, 1991; Gupta, 1977). When rehydrated mosses in these experiments were left in contact with the nutrient-laden water for multiple days, they reassimilated the majority of nutrients lost during rehydration (Brown & Buck, 1979; Gupta, 1977). While there may be some natural conditions when mosses remain in contact with nutrients lost during rehydration long enough to reassimilate them (e.g. immediately following small rain events), there are other plausible conditions that could transport some or all of the leaked nutrients away from rehydrating mosses and into the soil (e.g. larger rain events or osmotic/diffusive soil characteristics).

To our knowledge, two studies have measured nutrient releases from rehydrating mosses during rain events and found that resources lost from rehydrating mosses were leached from mosses in throughfall (Coxson, 1991; Wilson & Coxson, 1999). In the tropics, precipitation that passed through previously desiccated epiphytic bryophytes (one moss and one liverwort species) had more C, K and phosphorus than ambient rainfall and the composition and quantity of the throughfall C varied between bryophyte species (Coxson, 1991; Coxson, McIntyre, & Vogel, 1992). In a boreal forest, throughfall from desiccated specimens of the ground-dwelling feather moss

Hylocomium splendens contained higher C and K concentrations than ambient rainfall (Wilson & Coxson, 1999). The corresponding flux of C with K in the throughfall of rehydrated mosses found in both studies (Coxson, 1991; Coxson et al., 1992; Wilson & Coxson, 1999) suggests that the C loss accompanied cellular membrane damage. These studies did not, however, compare nutrient loss from hydrated mosses with that of rehydrated mosses to isolate the effect of desiccation and rehydration on these bryotic pulses, or consider the impact of lost nutrients on ecosystem processes.

Though untested, nutrient additions from bryotic pulses may influence soil C and N storage and cycling. For example, C released from bryotic pulses could increase pools of soil organic carbon or stimulate organic matter decomposition and result in a net loss of soil organic matter (Högberg & Ekblad, 1996). Nitrogen lost from rehydrated mosses to soil (Carleton & Read, 1991; Gupta, 1977) could further influence soil C and N cycling and lead to net N accumulation or net N loss in soil depending on the response of the soil microbial community. Furthermore, the addition of resources with high C:N ratios should increase soil CO₂ production while at the same time inhibiting soil nitrous oxide (N₂O) production (Baggs, Rees, Smith, & Vinten, 2000; Liang, Eberwein, Allsman, Grantz, & Jenerette, 2015). Finally, C and N accumulation or loss could be influenced by the chemistry of the C and N substrates themselves (Luo, Wang, & Sun, 2016; Morely & Baggs, 2010; Wang et al., 2015) which may vary across moss species and habitat types.

Here, we asked if desiccation and rehydration of mosses adds C and N to soil and if such C and N additions to soil drive net accumulation or loss of soil C and N. We selected eight species of moss that varied in habitat preference and life-form, the structure of a colony of individual shoots (Mägdefrau, 1982), from two temperate locations that differed in mean annual temperature and precipitation to evaluate the effects of desiccation and rehydration on bryotic pulses. We expected that mosses from the arid site would have a greater degree of desiccation tolerance, and experience less cellular damage during desiccation and less nutrient loss during rehydration than mosses from the mesic site. Likewise, we expected that mosses with tight cushion shaped life-forms, which often indicate habitat differences related to moisture and light (Glime, 2017; Proctor, 1990), would be more desiccation tolerant and lose fewer nutrients during rehydration. We quantified the effects of moss desiccation and rehydration on C and N fluxes by comparing C and N in the throughfall of hydrated versus rehydrated mosses in a greenhouse experiment. We also added the throughfall collected from four moss species, which were hydrated or rehydrated, to native soil in a laboratory experiment. We monitored soil respiration (CO₂) and nitrous oxide (N₂O) efflux, as these important loss pathways from incubation experiments may provide insight onto how C and N lost from bryotic pulses could alter soil C and N cycling. We hypothesized that throughfall C and N would have higher concentrations in the throughfall of rehydrated mosses than throughfall from hydrated mosses due to cellular damage incurred by mosses during desiccation and rehydration. If so, then the throughfall from rehydrated mosses, with more C and N than the throughfall of

hydrated mosses, should drive greater increases in soil microbial activity related to C (CO₂) and N (N₂O) cycling. We also hypothesized that throughfall with high C:N ratios would increase CO₂ efflux while at the same time inhibiting N₂O efflux. Though C and N interactions are complicated, high C:N conditions could induce microbial immobilization of inorganic N and result in low substrate availability for N₂O loss.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling regimes

We selected two temperate study sites that varied in mean annual temperature, rainfall and moss species composition, and with a high abundance of co-occurring mosses. Mosses were collected from roughly 200 ha of forest in northwestern Oregon (45°41'00.5"N, 121°44'50.8"W) and 400 ha of forest in west-central Montana (47°35'31.0"N, 115°13'44.9"W). Average annual temperatures near the Oregon site range from a high of 17.4°C to a low of 7.5°C with a mean annual rainfall of 95.3 cm (www.usclimatedata.com). The Montana site ranges in mean annual temperature from 14.5°C to 0.9°C and has a mean annual rainfall of 36.3 cm. Rainfall in both locations is highest in the spring and intermixed with multiday periods of dry weather, thus moss desiccation–rehydration events should correspond with high levels of spring plant and soil microbial activity.

2.2 | Throughfall analysis

We selected eight widespread ground-dwelling moss species that co-occur and vary in growth form and habitat preference to understand if these differences influenced nutrient losses during rehydration. *Kindbergia oregonum* and *Ceratodon purpureus* were collected from Oregon on 9 April 2014. *Aulacomnium palustre*, *Dicranum scoparium*, *Racomitrium lanuginosum*, *Rhytidiadelphus triquetrus*, *Plagiomnium ciliare* and *Syntrichia papillosum* were collected at the Montana site on 10 April 2014 (species identifications follow Flora of North America Editorial Committee, 2007,2014). All mosses were desiccated when harvested, and within 2 days, most of the plant debris and attached soil was removed by hand. Mosses were transplanted into 5 × 5 cm pots ($n = 16$ per species) filled with a homogeneous nutrient-poor substrate of sand/coir mixture (Down to Earth, Eugene, OR) at a ratio of 2:1 and placed into the University of Montana Dieltart Research Greenhouse.

Mosses were misted with tap water for 30 minutes four times a day for 2 days in an effort to remove soil, dust and atmospheric particulates from leaf surfaces (Coxson, 1991). After 48 hr, eight pots of each species were removed from the misting table and placed on a nearby table to dry for 7 days while the other eight pots were kept continuously hydrated for 7 days. To collect throughfall, moss was removed from a single pot and placed in a funnel attached by polyvinyl tubing to sterile 50-ml Falcon tubes and misted until 40 ml of throughfall was collected (adapted from

Coxson, 1991). Surface water was blotted from mosses and then mosses were weighed. Next, the lateral area of each moss sample was traced onto paper which was later measured with ImageJ (Rueden et al., 2017). We also ran tap water through empty funnels as controls for background nutrient levels. Non-purgeable organic carbon and total N of throughfall were determined with a Shimadzu TOC-V TN Analyzer (Shimadzu Corporation, Kyoto, Japan). Total amounts of C and N for hydrated and rehydrated mosses are presented by concentration in volumetric units (mg/L) and on an area basis (mg/cm²).

Mosses from Oregon versus Montana were likely to have been desiccated for different lengths of time prior to harvesting. However, by using field grown mosses, we assured that the mosses were acclimated (or hardened; see Stark, 2017) to natural conditions. Thus, the amount of nutrients lost from these mosses during rehydration should roughly reflect each species' evolutionary and environmentally determined abilities to survive cycles of desiccation and rehydration, or desiccation tolerance.

2.3 | Gas efflux from soil incubation

To explore the effects of nutrients released in the throughfall of hydrated or rehydrated moss on soil CO₂ and N₂O efflux, we collected and stored large quantities of throughfall from separate moss individuals in a similar manner as above and used the throughfall in a soil incubation experiment. We collected *Syntrichia*, *Rhytidiadelphus*, *Dicranum* and *Racomitrium* between June and August 2017 from the Montana site. Mosses were collected dry, cleaned and transplanted into the greenhouse within 48 hr. Mosses were planted in 5 × 5 cm pots ($n = 40$ per species) and misted four times a day for 9 days to maintain constant hydration. After 9 days, half of the pots for each species ($n = 20$ per species) were desiccated for 6 days while the other half remained continuously hydrated at the same misting rate. Throughfall was collected in the manner described above and frozen until use.

Soil samples for the experiment were collected on 11 September 2017, when soil was dry, from a forested area near Missoula, MT where all four species of moss from the arid site co-occurred (46°59'00.3"N, 114°01'35.1"W). Soils consisted of fine to gravelly, loamy Alfisols (www.websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx) and were collected to a depth of 12 cm, homogenized, and sieved through a 2-mm screen. On average, soils were 5.83% C and 0.25% N on a dry weight basis (mean C:N ratio of 23.5) (Eurovector elemental analyzer, Pavia, Italy) and had a mean gravimetric water content of 0.06 (g/g dry soil). Sixty grams of moistened soil (gravimetric water content increased to 0.2 [g/g dry soil]) was measured into specimen cups which were placed inside 45 1-L Mason jars prefilled with 5 ml of deionized water to ensure that soils maintained a constant moisture. Forty of the specimen cups were treated with 25 ml of throughfall, with five jars assigned for each species-treatment combination (hydrated vs. rehydrated for the four moss species). Five more soil samples were watered with 25 ml of deionized water as a control. Six additional jars were treated in the

same way as the experimental jars, but did not receive soil to account for gas concentrations in the laboratory environment. Mason jars were sealed with lids fitted with rubber septa for gas sampling and incubated at 22°C in darkness. We removed 15 ml gas samples from the jar headspace at three time points (6, 24 and 48 hr) and placed samples into 12-ml evacuated Exetainer vials (Labco Ltd., Buckinghamshire, UK). After the 6-, 12- and 48-hr sampling events, Mason jar lids were removed and lab air was pumped through the jars for 5 min to flush out existing gas in the jars prior to resealing. We calculated cumulative gas fluxes as the sum of the sampling events, as each sampling event represented the accumulation of gas since the last sampling event. Gas samples were analysed for CO₂ and N₂O concentrations using a Shimadzu GC-2014 greenhouse gas analyzer (Shimadzu Scientific, Kyoto, Japan). We present gas efflux as mass of C or N produced per soil dry weight. We did not standardize the amounts of C or N added to soils because we were interested in the general effects of the compounds carried in moss throughfall. Therefore, our results reflect the microbial response to C and N concentration, as well as the microbial response to C and N quality and C:N ratios.

2.4 | Data analyses

Differences in total organic carbon (TOC) concentrations between hydrated and rehydrated mosses were tested with a two-way ANOVA model after adjusting TOC concentrations for moss area or weight for all species combined with TOC concentration as the response variable, and species, treatment (hydrated or rehydrated) and their interaction as fixed factors. Total nitrogen (TN) concentrations in hydrated moss throughfall were below the detection limits of our machine (0.0001 mg/L). Thus, we were unable to compare differences in TN between throughfall treatments. Total nitrogen levels in the throughfall of rehydrated mosses were adjusted for moss area or weight and compared across species with a one-way ANOVA model where TN concentration was the response variable and species was a fixed factor.

The effect of bryotic pulses on soil CO₂ or N₂O efflux was evaluated with two-way ANOVAs. We treated the independent and interactive effects of moss species and moss desiccation treatment as fixed factors with the cumulative CO₂ and N₂O efflux (48 hr post-incubation) as response variables (two separate two-way ANOVAs) and with CO₂ and N₂O efflux at the 6- and 24-hr time points as response variables in four separate two-way ANOVAs. We used two tailed *t*-tests to evaluate if the addition of throughfall promoted differences in CO₂ and N₂O efflux within species by comparing treatment means to the mean of the water treatment for each time point.

We calculated net change in soil C and N as a measure of the effect of C or N in the throughfall from mosses on soil CO₂ or N₂O efflux respectively. Net change in soil C and N was determined by subtracting the gas efflux of water treated soil (control) from throughfall treated soil and then subtracting this from the total amount of C or N added in throughfall (from TOC (mg C g soil⁻¹) and TN values (ng N g soil⁻¹); Equations 1 and 2):

$$\text{NetC change} = (\text{throughfall C}) - (\text{CO}_2 \text{ efflux treatment} - \text{CO}_2 \text{ efflux control}) \quad (1)$$

$$\text{NetN change} = (\text{throughfall N}) - (\text{N}_2\text{O efflux treatment} - \text{N}_2\text{O efflux control}) \quad (2)$$

A positive net C or N change represents throughfall C or N that is retained in soil (not lost as CO₂ or N₂O) in the first 48 hr after addition to soil. By contrast, a negative net C or N change suggests that the addition of throughfall C or N to soil causes an efflux of more C as CO₂ or N as N₂O than was added, meaning extant soil C or N was lost in the first 48 hr after throughfall was added.

Two-way ANOVAs were used to evaluate the independent and interactive effects of moss species and desiccation treatment as fixed factors on the response variables net change in soil C and N. The effects of throughfall treatments on net change in soil C and N within study species were compared with one-way ANOVAs with net C or N change as a response variable and throughfall treatment (hydrated or rehydrated) as a fixed factor.

Pearson's product-moment correlations were used to evaluate relationships between the variables: throughfall C, throughfall N, throughfall C:N ratio, cumulative CO₂ efflux and cumulative N₂O efflux. Since total nitrogen (TN) concentrations in hydrated moss throughfall were at or below the detection limits of our machine (0.0001 mg/L), we used this value to calculate C:N ratios for hydrated moss throughfall. All analyses were performed in JMP, Version 11.0 (SAS Institute Inc., Cary, NC, 2013). Prior to analyses, distributions of means were checked for normality using the Shapiro–Wilk test. TOC and TN concentrations were log-transformed and CO₂ efflux and net change in soil C were exponentially transformed to satisfy assumptions of normality and homoscedasticity.

3 | RESULTS

3.1 | Throughfall analysis

Rehydrated mosses generated throughfall with 7–77 times more C, by area, ($F_{1,124} = 304$, $p < 0.0001$, Figure 1), and 11–80 times more C by weight, than hydrated mosses (Figure S1, Table S1), depending on the species. The quantity of TOC in the throughfall of hydrated or rehydrated mosses also varied among species ($F_{7,110} = 2.33$, $p = 0.0296$). For most moss species, TN was not detectable in the throughfall of hydrated mosses (Figure 1, Figure S1). TN in the throughfall of rehydrated mosses ranged from 0 to 0.71 mg/L (Table 1), but did not differ statistically among species ($F_{6,33} = 0.28$, $p = 0.9407$, Figure 1, Figure S1). Throughfall C:N ratios from rehydrated mosses ranged from 33 to 331 mg/L (Table 1).

3.2 | Soil incubation gas efflux

The effects of throughfall on soil CO₂ efflux were substantial early in our incubation but declined over 48 hr. After 6 hr of incubation,

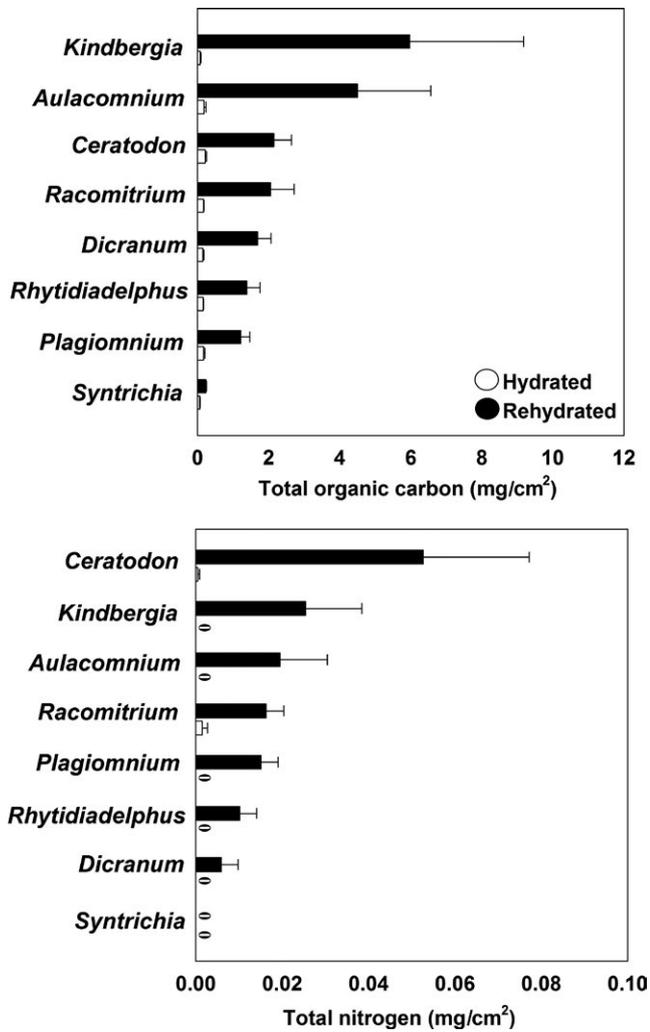


FIGURE 1 Total organic carbon and total nitrogen in throughfall of hydrated (open bars) or rehydrated (filled bars) mosses by moss area. Bars show means + SE

throughfall from all species of hydrated and rehydrated mosses significantly increased soil CO₂ efflux rates relative to the effect of water additions alone (Figure S2, Table S3). The effect of throughfall on soil CO₂ efflux after 6 hr of incubation varied by moss species from which the throughfall was derived ($F_{3,32} = 3.340$, $p = 0.0310$) but not by throughfall type (hydrated or rehydrated; Table S2), and there was no significant interaction between moss species and the throughfall treatment (Table S2). After 24 hr of incubation, the effect of moss species on soil CO₂ efflux disappeared, and there were no significant effects of the throughfall treatment or moss species by throughfall treatment interactions (Table S2). Relative to the effect of water alone, throughfall from hydrated *Dicranum* and *Rhytidiadelphus* and rehydrated *Syntrichia* and *Dicranum* significantly increased soil CO₂ efflux rates 24 hr after incubation (Table S3). Cumulatively, 48 hr after incubation, moss throughfall from hydrated *Dicranum* and *Rhytidiadelphus* and rehydrated *Dicranum* increased soil CO₂ efflux relative to the effect of water additions alone (Table S3). However, there were no significant differences among moss species and between

TABLE 1 Mean concentrations of total organic carbon, total nitrogen, and the carbon to nitrogen ratio (C:N) in the throughfall of mosses that were desiccated and rehydrated during a single simulated rain event

Species	Total C (mg/L)	Total N (mg/L)	C:N
<i>Kindbergia oregonum</i>	179	0.54	331
<i>Aulacomnium palustre</i>	42.4	0.24	177
<i>Ceratodon purpureus</i>	23.2	0.71	33
<i>Plagiomnium ciliare</i>	20.0	0.25	80
<i>Dicranum scoparium</i>	27.1	0.09	301
<i>Racomitrium laniginosum</i>	94.2	0.71	133
<i>Rhytidiadelphus triquetrus</i>	47.8	0.42	114
<i>Syntrichia papillosissima</i>	5.63	0	—

throughfall treatments on soil CO₂ efflux, and there was no significant species by throughfall treatment interaction (Table S2).

Throughfall from hydrated and rehydrated mosses varied in their influence on soil N₂O efflux 6 hr after incubation. Throughfall from hydrated *Syntrichia*, *Dicranum* and *Rhytidiadelphus* and rehydrated *Syntrichia* significantly decreased soil N₂O efflux after 6 hr relative to the effect of water alone (Figure S2, Table S3). Six hours into the incubation, the effect of throughfall on soil N₂O efflux rates differed significantly among moss species ($F_{3,32} = 3.36$, $p = 0.0308$) and between throughfall treatments ($F_{1,32} = 23.9$, $p < 0.0001$) but there was no interaction of moss species and throughfall treatment (Table S2). Twenty-four and forty-eight hours into the incubation, the addition of hydrated and rehydrated moss throughfall significantly increased soil N₂O efflux relative to water for all moss species (Figure 2, Figure S2, Table S3). Additionally, 24 hr into the incubation, there were significant differences among moss species ($F_{3,32} = 9.12$, $p = 0.0002$) and between throughfall treatments ($F_{1,32} = 22.0$, $p < 0.0001$) on soil N₂O efflux, and there was a significant moss species by throughfall treatment interaction ($F_{3,32} = 7.15$, $p = 0.0008$; Table S2). After 48 hr, the cumulative soil N₂O efflux significantly differed by moss species ($F_{3,32} = 3.92$, $p = 0.0173$) and throughfall treatment ($F_{1,32} = 5.31$, $p = 0.0279$), but there was no significant moss species by throughfall treatment interaction (Figure 2, Table S2).

Throughfall effects on the net change in soil C were varied among moss species ($F_{3,32} = 31.4$, $p < 0.0001$; Equation 1; Figure 3) and by the two types of moss throughfall ($F_{1,32} = 60.4$, $p < 0.0001$). There was also an interaction among moss species and throughfall treatment on the net change in soil C ($F_{3,32} = 31.0$, $p < 0.0001$). For three of four moss species, more net C immobilization occurred in soils exposed to throughfall from rehydrated mosses while throughfall from hydrated mosses promoted net C mineralization (*Racomitrium*: $F_{1,8} = 42.1$, $p = 0.0002$; *Dicranum*: $F_{1,8} = 12.1$, $p = 0.0084$; *Rhytidiadelphus*: $F_{1,8} = 18.8$, $p = 0.0025$).

The effect of throughfall on the net change in soil N varied among moss species ($F_{3,32} = 98,511$, $p < 0.0001$, Equation 2; Figure 3) and by the two types of moss throughfall ($F_{1,32} = 269,425$, $p < 0.0001$). There was also an interaction among moss species and throughfall treatments on the net change in soil N ($F_{3,32} = 72,032$, $p < 0.0001$). For

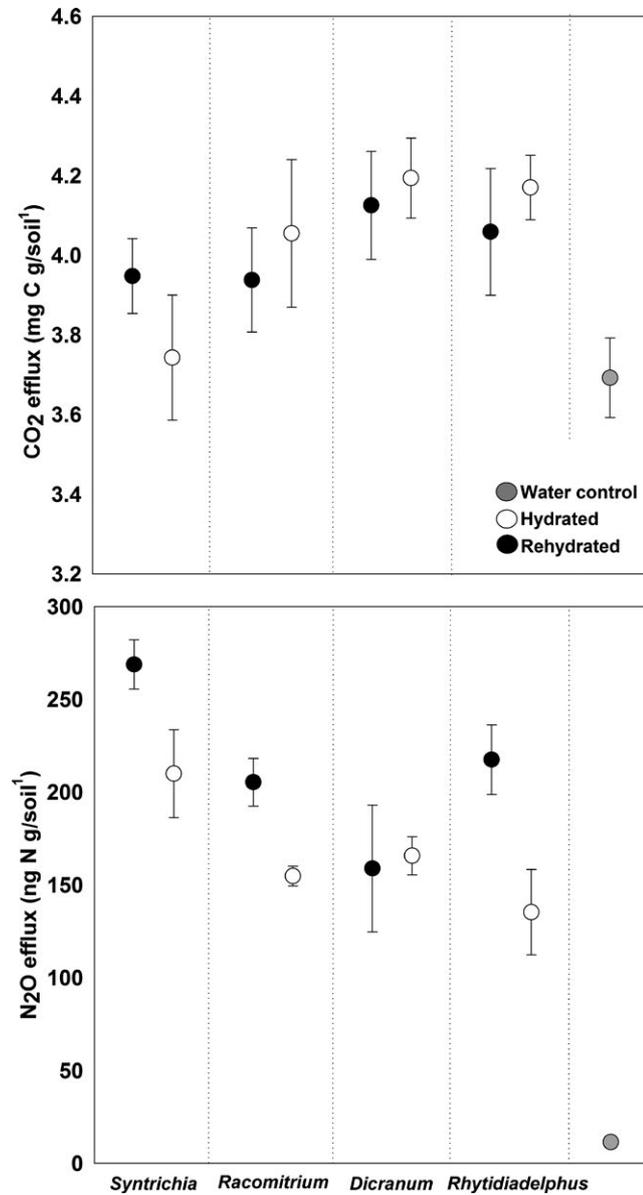


FIGURE 2 CO_2 and N_2O efflux over a 48 hr incubation of soil treated with throughfall or water (control). Throughfall from four species of moss was collected after passing through hydrated mosses (open circles) or as mosses were rehydrated from a desiccated state (filled circles). Data show means \pm SE

three moss species, more net N immobilization occurred in soils exposed to throughfall from rehydrated as compared to hydrated mosses (*Dicranum*: $F_{1,8} = 4,200$, $p < 0.0001$; *Racomitrium*: $F_{1,8} = 1,343,097$, $p < 0.0001$; *Rhytidiadelphus*: $F_{1,8} = 124,382$, $p < 0.0001$).

There was no relationship between throughfall C and the cumulative CO_2 or N_2O efflux (CO_2 efflux: $r = -0.06$, $p = 0.7309$; N_2O efflux: $r = 0.14$, $p = 0.3899$; Figure 4a,d) or throughfall N and the cumulative CO_2 or N_2O efflux (CO_2 efflux: $r = -0.04$, $p = 0.7882$; N_2O efflux: $r = 0.28$, $p = 0.0775$; Figure 4b,e). The throughfall C:N ratio was not related to the cumulative CO_2 efflux ($r = 0.16$, $p = 0.3230$) but the cumulative N_2O efflux was negatively associated with the throughfall C:N ratio ($r = -0.38$, $p = 0.0142$; Figure 4c,f).

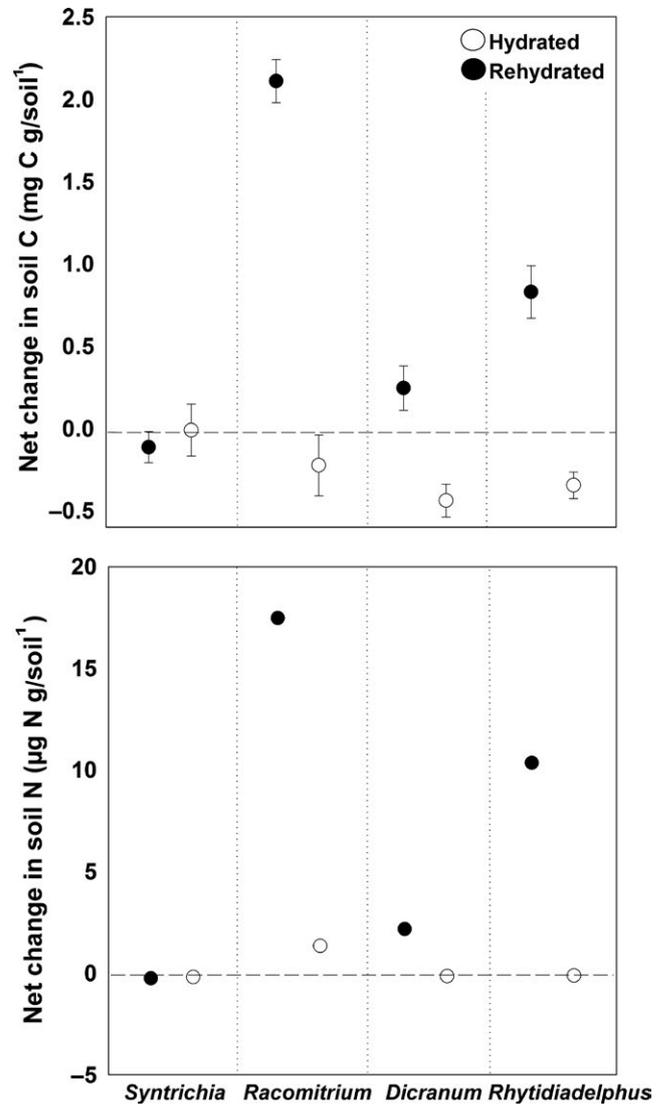


FIGURE 3 Net soil C and N change generated from the addition of moss throughfall to soil. Throughfall was collected from four species of moss that were hydrated (open circles) or as they were rehydrated from a desiccated state (filled circles). We used a mass-based approach to calculate net change in C and N by subtracting the gas efflux of control (water only) treated soil from throughfall-treated soil and then subtracting this from the total amount of C or N added in throughfall (Equations 1 and 2). Data show means \pm SE. Error bars for net N change are within the symbols

4 | DISCUSSION

Our results identify a potentially important mechanism by which mosses might influence ecosystem processes and properties. Cellular damage in mosses incurred during our desiccation and rehydration treatments resulted in the loss of far more C and N in the throughfall of rehydrated mosses than that of hydrated mosses, and throughfall from rehydrated mosses produced novel soil C and N flux responses. The magnitude of C and N in these *single* simulated bryotic pulses, estimated by area, was roughly equivalent to the *annual* throughfall C and N fluxes from boreal trees (N: 0.68 g/m^2 ; Blew, Iredale, & Parkinson, 1993; C: 31.3 g/m^2 , N: 7.8 g/m^2 ; Mellec,

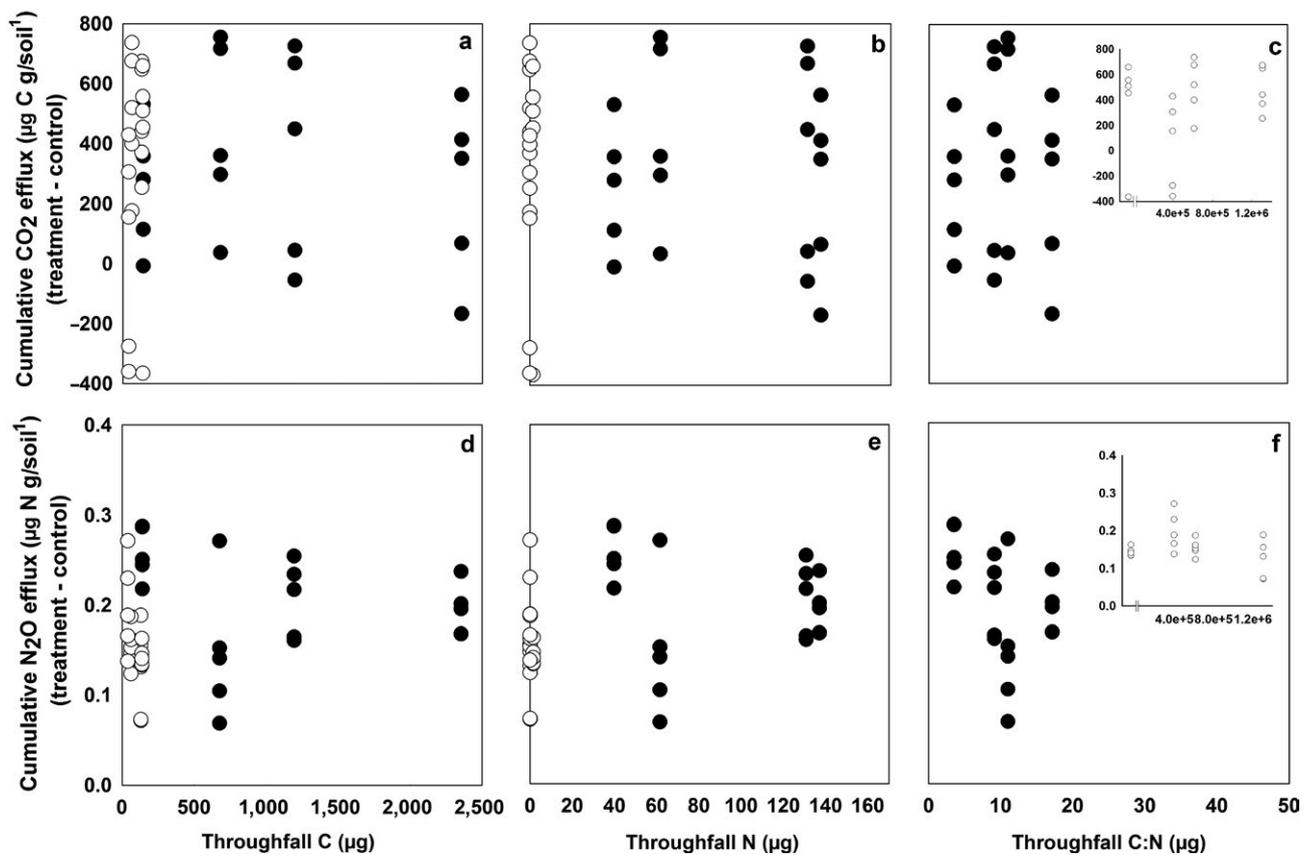


FIGURE 4 Relationships between throughfall C, N and C:N ratio and the effect of throughfall on the cumulative CO_2 (a, b, c) and N_2O (d, e, f) efflux. The cumulative effect of throughfall on CO_2 and N_2O efflux was calculated by subtracting the gas efflux of control (water only) treated from throughfall treated soil after a 48 hr incubation. The throughfall and amount of gas produced from hydrated mosses is shown with open circles and rehydrated mosses with filled circles. When present, panel inserts (c, f) display hydrated moss relationships only with X-axes scaled to fit the data

Meesenburg, & Michalzik, 2010) and temperate deciduous forests (N: 0.88 g/m^2 ; Carlisle, Brown, & White, 1966; C: 13 g/m^2 , N: 0.7 g/m^2 ; Qualls, Haines, & Swank, 1991). This reinforces and quantifies the potential importance of desiccation and rehydration as a mechanism driving the general effects of mosses on ecosystems, and suggests that moss desiccation and rehydration should be considered when evaluating the effects of mosses on soil C and N cycling. That said our laboratory results must be followed by field measurements in order to provide more evidence that this mechanism is equally strong in natural ecosystems.

Two moss species included in this study, *Ceratodon* and *Syntrichia*, are common dryland mosses and components of biological soil crusts (biocrusts hereafter). Biocrusts are well recognized for their role in global biogeochemical C and N cycles (Delgado-Baquerizo et al., 2016; Elbert et al., 2012) but the direct contribution of C and N from the desiccation and rehydration of biocrust mosses has not been incorporated into the well-recognized biogeochemical role of biocrusts in ecosystems. Nutrients lost from rehydrating biocrust mosses may also be transferred to nearby vascular plants through soil fungi (for the fungal loop hypothesis, see Aanderud et al., 2018; Collins et al., 2008; Dettweiler-Robinson, 2018; Green, Porrás-Alfaro, & Sinsabaugh, 2008) but this has not been tested. Finally,

since the impact of mosses on soil N and C cycling is regulated by climate, changing climate conditions that alter the frequency and duration of bryotic pulses will directly influence how mosses interact with soil N and C cycling.

4.1 | Rehydration and resource release

Throughfall from rehydrated mosses often contained an order of magnitude more C than the throughfall of hydrated mosses, but this difference varied dramatically among moss species. Variation among species may be due to how different moss species utilize C compounds for cellular protection throughout the desiccation and rehydration processes (see Hoekstra, Golovina, & Buitink, 2001; Oliver et al., 2005; Green et al., 2011; Stark, 2017). For example, C compounds are thought to replace water molecules in the cell membrane during desiccation to stabilize the membrane and prevent fracturing (Crowe, Hoekstra, & Crowe, 1992; Hoekstra et al., 2001; Smirnov, 1992). Mosses also rely on C compounds for intracellular osmotic adjustment during the initial stages of drying, and as desiccation proceeds and molecular mobility in the cytoplasm decreases, cytoplasmic C compounds facilitate the transition of the cytoplasm into a glassy brittle phase to prevent cellular

collapse and protein denaturing (Hoekstra et al., 2001; Koster, 1991; Sun & Leopold, 1997). Finally, mosses rely on a variety of C compounds to scavenge reactive oxygen species which increase in abundance during water stress (Popp & Smirnov, 1995; Smirnov & Cumbes, 1989). Variation in the ways different moss species utilize carbon compounds to ensure survival may explain why species vary considerably in the types and amounts of C they contain (Robinson, Wasley, Popp, & Lovelock, 2000) and release. We do not know of comparisons of the types of C compounds contained or released by moss species across environments, but species from arid environments are thought to be more desiccation tolerant with fine-tuned suites of morphological, physiological and molecular strategies that minimize the loss of cellular compounds during rehydration (Brown & Buck, 1979). It is possible that variation in these adaptations contribute to differences among moss species in the quality and quantity of C (and N) lost during rehydration in bryotic pulses.

Our study captured element loss from mosses during one simulated rain event, but naturally occurring rehydration events may vary widely in intensity, frequency and duration, and this may lead to different amounts of C or N loss in throughfall. Element loss from mosses during rehydration is determined by the level of cellular damage incurred during desiccation and rehydration; thus, very intense periods of desiccation may promote greater resource loss due to the intensity of cellular damage and lead to an increase in time needed for cellular repair (reviewed in Oliver, 2008). However, the strategies utilized by mosses to survive repeated cycles of drying and wetting are determined by both the evolutionary history of a species and their short term environmental history. Hence, mosses that live in habitats that require a higher degree of desiccation tolerance should experience less damage during desiccation and less element loss during rehydration than mosses adapted to less environmentally stressful conditions (Dilks & Proctor, 1974; Green et al., 2011). Our results generally support this hypothesis with genera of mosses known to be more desiccation tolerant like *Syntrichia* losing much less C and N during rehydration than less desiccation tolerant mosses like *Kindbergia*. However, *Kindbergia* lost 87% more C in throughfall when rehydrated than *Ceratodon* (from the same location in Oregon), suggesting that in addition to local adaptation to climate other factors may also influence the ability of individual species to avoid membrane damage and resource loss associated with desiccation and rehydration. In the future, comparisons of dehardened mosses with their environmental history removed and hardened mosses with their environmental history intact could be used to determine the intrinsic effects (dehardened mosses) of desiccation and rehydration on C and N loss from those that are environmentally determined (hardened mosses; see Stark, 2017). In this context, the ecological relevance of our results are reasonably strong as we used field hardened mosses and experimentally exposed them to a low stress slow-drying experience (7 days of drying; Stark, 2017) prior to rehydration which should cause less cellular damage.

Variation in C and N loss among moss species following desiccation and rehydration may also be affected by life-form (Mägdefrau,

1982), or the overall structure of a colony of individual shoots, which provides an indication of habitat differences related to moisture and light (Glime, 2017; Proctor, 1990). For instance, species with loose trailing life-forms are more common in moist forests, whereas tight cushion forming mosses are typical of exposed sites subject to frequent drying (Glime, 2017). *Kindbergia* and *Ceratodon*, from our Oregon site, have very different life-forms. *Kindbergia* occurs in the understory of dense forests and has creeping stems that generate loose tufts of fronds (Ignatov, 2014), whereas *Ceratodon* dwells in a variety of habitats from exposed roadsides to forest understory and forms short turfs (McIntosh, 2007). Turf-forming mosses like *Ceratodon* may be able to retain more water and elements in the interspaces of shoots than loose feather mosses like *Kindbergia* and this may account for some of the differences in C loss measured here. Alternately, but not mutually exclusive, tighter life-forms like *Ceratodon* may be more desiccation tolerant than loose trailing life-forms like *Kindbergia* and lose fewer elements during rehydration.

4.2 | Influence of bryotic pulses on soil C and N cycling

Moss throughfall C and N concentrations altered soil C and N cycling in our laboratory based study. Based on stoichiometric principles, we expected throughfall with a high C:N ratio to increase soil CO₂ efflux and inhibit soil N₂O efflux, and we expected that throughfall with a low C:N ratio would increase N₂O efflux and decrease CO₂ efflux (Baggs et al., 2000; Liang et al., 2015). In addition to the effect of resource stoichiometry, soil CO₂ and N₂O efflux should also be influenced by the quantity and species-specific chemistry of the C and N substrates (Luo et al., 2016; Morely & Baggs, 2010; Wang et al., 2015).

In general, moss throughfall had a positive effect on soil CO₂ and N₂O efflux, regardless of whether the moss was hydrated or rehydrated. But contrary to a previously reported positive relationship between C addition and soil CO₂ efflux (e.g., Högberg & Ekblad, 1996), throughfall from different species of hydrated or rehydrated mosses had similar effects on soil CO₂ efflux despite very large differences in the quantities of C and N added to soils in throughfall. The addition of throughfall from hydrated mosses, with higher C:N ratios than throughfall from rehydrated mosses, generated lower soil N₂O efflux than the throughfall of rehydrated moss for three of four moss species. These results are supported by others which found that the addition of substrates with high C:N ratios reduced soil N₂O efflux (Baggs et al., 2000; Liang et al., 2015). We also found that the highest rate of soil N₂O efflux occurred from adding the throughfall of rehydrated *Syntrichia*, the species of moss that lost the least C and no detectable N during rehydration. Therefore, it is likely that the quality of C in moss throughfall may have influenced soil N transformations and N₂O efflux more than the quantity of C. There are many soil N transformation pathways that generate N₂O (reviewed in Butterbach-Bahl, Baggs, Dannenmann, Kiese, & Zechmeister-Boltenstern, 2013) but two are most likely to be relevant here. N₂O can be produced as a byproduct of the anaerobic process of denitrification or of the aerobic process of nitrifier denitrification, as both

processes are regulated by N, C and water availability (Bremner, 1997; Tiemann & Billings, 2008). Though our soil incubations were probably not anaerobic, small anaerobic microsites may have existed, making it impossible in this study to separate the relative roles of anaerobic denitrification and aerobic production of N_2O from nitrification. Mosses affect N accumulation (Bowden, 1991; Hu, Wang, Pan, Zhang, & Zhang, 2014), N storage (Oechel & Van Cleve, 1986), N fixation (Deane-Coe et al., 2015; DeLuca, Zackrisson, Nilsson, & Sellstedt, 2002), N_2O emissions (Porada, Pöschl, Kleidon, Beer, & Weber, 2017) and N availability (Delgado-Baquerizo et al., 2016; Lindo & Gonzales, 2010). However, the effect of nutrient loss from mosses following desiccation and rehydration on soil N pools and fluxes may represent a new pathway by which mosses could influence the soil environment, and one that might revise previous estimates.

Contrary to our predictions, we found that soils incubated with throughfall derived from hydrated mosses with lower C concentrations and no detectable N resulted in more C emitted from soil as CO_2 than was added in throughfall which could generate a net loss of soil C. Throughfall from rehydrated mosses, which had higher C and N concentrations than throughfall from hydrated mosses, resulted in less CO_2 produced than the amount of C added in throughfall—conditions more likely to increase soil C. Additionally, there was no relationship between the quantity of throughfall C or N added from hydrated and rehydrated mosses on cumulative soil CO_2 efflux. The quality or chemistry of C released in bryotic pulses might affect particular groups of microbes differently based on their substrate preference (Luo et al., 2016; Six & Jastrow, 2002; Wang et al., 2015). Longer term and in situ studies will be needed to confirm how bryotic pulses influence soil C pools, but the addition of recalcitrant or complex C compounds in throughfall during rehydration could be a mechanism by which mosses may increase soil organic matter accumulation (Gornall et al., 2007; Lamontagne, 1998; Sedia & Ehrenfeld, 2005; Sun et al., 2017; Zhao et al., 2014).

The difference between the amount of N added in throughfall and the amount of N lost as N_2O after throughfall addition varied in our study depending on moss species and whether soils received throughfall from hydrated or rehydrated mosses. With the exception of *Racomitrium*, soils treated with throughfall from hydrated mosses released a similar amount of N as N_2O than was added in throughfall which means that throughfall from hydrated mosses is unlikely to change soil N. However, with the exception of *Syntrichia*, more N was added in the throughfall of rehydrated mosses than was lost as N_2O after the addition of rehydrated moss throughfall to soil; a situation that could result in an increase in soil N. Interestingly, increasing concentrations of throughfall C and N from both rehydrated and hydrated mosses had no influence on cumulative N_2O efflux. This was most likely related to the throughfall C. For the most part, throughfall with little to no N (e.g. hydrated moss throughfall) had little to no effect on soil N and resulted in a net loss of soil C. Similarly, throughfall from rehydrated *Dicranum* with a higher C:N ratio had a more negative effect on the change in soil N than throughfall from rehydrated *Rhytidiadelphus* and *Racomitrium* with lower C:N ratios.

This suggests that changes in soil C are, in part, driven by N limitation. This result underscores another potential biogeochemical role of mosses in ecosystems. When mosses produce throughfall with relatively higher amounts of C and N, C and N could be retained in the ecosystem. Additionally, when mosses produce throughfall with little N but some C, more soil C may be lost from soil than added in throughfall. Mosses have been positively associated with soil N availability and N transformation rates (Gornall et al., 2007; Hu et al., 2014; Sedia & Ehrenfeld, 2005) but the mechanistic underpinnings of these associations are poorly understood. Our finding that moss desiccation and rehydration can change the effect of mosses on soil N and C cycling has not previously been observed.

5 | CONCLUSIONS

Our results suggest that relatively large amounts of C and N released from mosses during desiccation and rehydration cycles are an important means by which mosses might alter soil C and N pools. The quantity of TOC in the throughfall of rehydrated mosses was 2–31 mg/cm^2 times greater than the amount of TOC in the throughfall of hydrated mosses. Throughfall TOC from rehydrated mosses also varied substantially among the eight species of mosses tested. Throughfall from hydrated mosses had little to no TN, whereas throughfall TN levels were consistent among species of rehydrated mosses. Throughfall from rehydrated mosses differed from the throughfall of hydrated mosses in its effect on soil gas efflux in most cases. We found that the throughfall from rehydrated mosses promoted higher soil N_2O efflux than the throughfall of hydrated mosses. Additionally, throughfall of rehydrated mosses generated positive changes in soil C and N while the throughfall of hydrated mosses generated negative changes in soil C and had no effect on soil N. The intensity of the effects of throughfall from hydrated and rehydrated mosses on soil gas efflux varied among moss species, and in a manner that suggests that the quantity and quality of C and N compounds carried in moss throughfall may drive variation in the effects of throughfall on soil biota and subsequently soil C and N pools.

We highlight that in situ and longer term studies are necessary to fully understand the implications of this work across the diverse communities and ecosystems in which mosses occur. In particular, field based studies that incorporate established mosses and quantify C and N loss from mosses in relation to natural variation in the frequency, quantity and duration of rainfall will elucidate more realistic connections between desiccation damage and C and N loss from mosses in bryotic pulses. Additionally, the rate of cellular repair following rehydration directly determines the duration of bryotic pulses, but the duration of this period of repair is known for only a few moss species for which repair rates varied from 30 min to 12 hr (Coxson et al., 1992; Oliver, Mishler, & Quisenberry, 1993; Wilson & Coxson, 1999). Integration of such data with existing models of moss effects on ecosystems (e.g., Delgado-Baquerizo et al., 2016; Porada et al., 2017; Sun et al., 2017) could allow us to determine the effects of mosses on soil C and N pools and fluxes and

understand how changing environmental patterns will influence moss-mediated nutrient cycling. This may be of particular importance in systems where predicted increases in temperature and changes in precipitation patterns may cause widespread increases in moss mortality and yield large changes in C and N budgets (Barker, Stark, Zimpfer, Mclethie, & Smith, 2005; Belnap, Phillips, Flint, Money, & Caldwell, 2008; Coe, Belnap, & Sparks, 2012; Li, Jia, Zhang, Zhang, & Hui, 2018; Reed et al., 2012).

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AUTHORS' CONTRIBUTIONS

This study was designed by all authors. M.L.S. performed the experiments. M.L.S. and B.W.S. conducted laboratory analyses and M.L.S. analysed the data. M.L.S. wrote the manuscript with significant contributions from both co-authors.

DATA ACCESSIBILITY

Data associated with this research has been deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.vc1s9f3> (Slate, Sullivan, & Callaway, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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