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RESEARCH REVIEW

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Empirical and Earth system model estimates of boreal nitrogen fixation often differ: A pathway toward reconciliation

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Abstract

The impacts of global environmental change on productivity in northern latitudes will be contingent on nitrogen (N) availability. In circumpolar boreal ecosystems, nonvascular plants (i.e., bryophytes) and associated N_2-fixing diazotrophs provide one of the largest known N inputs but are rarely accounted for in Earth system models. Instead, most models link N_2-fixation with the functioning of vascular plants. Neglecting nonvascular N_2-fixation may be contributing toward high uncertainty that currently hinders model predictions in northern latitudes, where nonvascular N_2-fixing plants are more common. Adequately accounting for nonvascular N_2-fixation and its drivers could subsequently improve predictions of future N availability and ultimately, productivity, in northern latitudes. Here, we review empirical evidence of boreal nonvascular N_2-fixation responses to global change factors (elevated CO_2, N deposition, warming, precipitation, and shading by vascular plants), and compare empirical findings with model predictions of N_2-fixation using nine Earth system models. The majority of empirical studies found positive effects of CO_2, warming, precipitation, or light on nonvascular N_2-fixation, but N deposition strongly downregulated N_2-fixation in most empirical studies. Furthermore, we found that the responses of N_2-fixation to elevated CO_2 were generally consistent between models and very limited empirical data. In contrast, empirical-model comparisons suggest that all models we assessed, and particularly those that scale N_2-fixation with net primary productivity or evapotranspiration, may be overestimating N_2-fixation under increasing N deposition. Overestimations could generate erroneous predictions of future N stocks in boreal ecosystems unless models adequately account for the drivers of nonvascular N_2-fixation. Based on our comparisons, we recommend that models explicitly treat nonvascular N_2-fixation and that field studies include more targeted measurements to improve model structures and parameterization.

KEYWORDS
boreal, bryophyte, diazotroph, Earth system model, elevated CO_2, nitrogen deposition, nitrogen fixation, nonvascular

1 | INTRODUCTION

Global environmental change is predicted to alter carbon (C) and nutrient cycles in northern latitudes, including boreal ecosystems (Coa & Woodward, 1998; Finzi et al., 2011; IPCC, 2018). The circumpolar boreal region is poised to undergo substantial modifications in C and nitrogen (N) cycling (Gillett et al., 2004; Walker et al., 2019), which could accompany shifts in vegetation composition, tree cover, and productivity. Warming and elevated CO_2 concentrations are expected to promote plant growth in boreal ecosystems but evidence suggests any positive growth response is likely to be dependent on N availability, which is typically very low in boreal ecosystems (Wieder, Cleveland, Smith, et al., 2015). Nitrogen availability could be further suppressed if greater C fixation by plants under elevated atmospheric CO_2 increases C relative to N in plant tissue, thereby increasing litter and organic C:N, as suggested by the progressive nitrogen limitation hypothesis (Hungate et al., 2003; Luo et al., 2004). Although forest warming experiments suggest enhanced plant growth (Melillo et al., 2011; Reich et al., 2015), free-air CO_2 enrichment experiments have shown little long-term benefit to plant growth without concurrent N enrichment (Jiang et al., 2020; Reich et al., 2006), suggesting that ecosystems may become increasingly N-limited under elevated CO_2 unless primary N inputs can keep pace with increasing carbon fixation.

Biological nitrogen inputs in boreal ecosystems, and conifer-dominated forests in particular, are derived primarily from epiphytic diazotrophs that reside on bryophyte foliar tissue (DeLuca et al., 2002; Houseman et al., 2020; Lindo et al., 2013). Bryophytes often comprise 70%–100% of ground cover in boreal forests, and can fix upwards of 2–3 kg N ha^{-1} $year^{-1}$ (DeLuca et al., 2002; Lagerström et al., 2007; Rousk et al., 2013; Zackrisson et al., 2004). In contrast, vascular N_2-fixing plants such as *Alnus* spp., *Lupinus* spp., and other legumes have a narrow distribution and abundance in the boreal region, and are generally limited to riparian areas or non-forested open habitats, respectively (Högberg et al., 2017; Houseman et al., 2020). Inorganic products of bryophyte–diazotroph N_2-fixation (NH_3 and NH_4^+) are available for uptake by the diazotroph or its host bryophyte (Bay et al., 2013), and can enter the soil N pool via decomposition or nutrient leaching (Slate et al., 2019). In boreal conifer forests, bryophytes account for far more stand-level N_2-fixation than vascular plants and free-living soil N_2-fixers (Houseman et al., 2020), and account for up to 92% of stand-level N requirements (Jean et al., 2018), highlighting their role as the primary source of biological N_2-fixation in most boreal ecosystems. However, bryophyte–diazotroph niches are subject to wide fluctuations in precipitation, temperature, and light (via shading), which directly and indirectly influence rates of N_2-fixation (Gundale, Nilsson, et al., 2012; Gundale, Wardle, et al., 2012; Sorensen et al., 2012). Moreover, elevated CO_2 and N deposition comprise additional global change factors that could generate shifting patterns of bryophyte–diazotroph N_2-fixation in boreal ecosystems (Carrell et al., 2019; Gundale et al., 2013). Although bryophyte N_2-fixation is occasionally considered to be decoupled from soil N pools (Lindo & Gonzalez, 2010), adequately accounting for its drivers could help improve predictions of N inputs via decomposition or leaching, and ultimately, ecosystem N cycling.

Earth system models and their land surface modeling components can predict ecosystem responses to global change factors at global or biome-specific scales. Land surface models did not include N cycling until Hungate et al. (2003) demonstrated that model predictions of terrestrial C uptake were unrealistically high because they failed to account for N constraints on tree growth. As a result, most land surface models now include coupled C-N cycling, with biological N_2-fixation as the main N input (Cleveland et al., 1999; Wieder, Cleveland, Lawrence, et al., 2015). However, accounting for biological N_2-fixation remains challenging in these models. A common approach is to use *regression-type* models, which correlate all sources of N_2-fixation (i.e., asymbiotic and symbiotic combined) with other ecosystem mass fluxes such as net primary productivity (NPP) or actual evapotranspiration (AET, Cleveland et al., 1999). For example, three of the five terrestrial models included in the Coupled Model Intercomparison Project (CMIP) link biological N_2-fixation using only NPP or AET based on these relationships. Emerging *homeostatic-type* models, on the other hand, replace the correlational relationship between N_2-fixation and NPP or AET with more process-based functions using plant N requirements and are further linked to C expenditure, light and temperature, and associated investment into plant tissue (e.g., Rastetter et al., 2001).

There is growing recognition that models need to account for potentially contrasting responses of vascular versus nonvascular (e.g., bryophyte–diazotroph) N_2-fixation to different scenarios, especially considering that nonvascular N_2-fixation can serve as the dominant form of N input in key biomes (e.g., boreal forests). N_2-fixing bacteria living in symbiosis with vascular plants (e.g., *Frankia* bacteria in symbiosis with *Alnus* spp.) can fix upwards of 100 kg N ha^{-1} $year^{-1}$ but are not as widespread as N_2-fixing bryophyte–diazotrophs in boreal ecosystems (Houseman et al., 2020; Rousk et al., 2014a). Partitioning N_2-fixation into vascular and nonvascular sources therefore allows models to account for different controlling factors, such as host carbon partitioning or environmental variables (Davies-Barnard & Friedlingstein, 2020; Lawrence et al., 2019). For example, the mechanistic nature of C and N exchange in bryophyte–diazotroph associations is unresolved, and may or may not involve a direct transfer of C from bryophytes to associated diazotrophs (Stuart et al., 2020). Consequently, even models that include a C expenditure for N uptake may not adequately account for the widespread bryophyte–diazotroph N_2-fixing niche. Moreover, bryophytes are poikilohydric; without stomata or cuticles, bryophytes have high desiccation tolerance and rapid recovery when rehydrated. This crucial physiological trait represents a fundamental difference from vascular plants that makes bryophyte productivity unsuitable for scaling with NPP or AET (Turetsky, 2003). Ultimately, despite the great importance of bryophyte–diazotroph N_2-fixation in northern latitude biomes and its fundamental difference from vascular N_2-fixation, the exclusion of bryophyte–diazotroph N_2-fixation from Earth system models suggests that model N_2-fixation schemes do not adequately reflect the response of N_2-fixation in these biomes to global change factors.

In this review, we (1) discuss the representation of biological N_2-fixation in Earth system models; (2) compare global and boreal-specific biological N_2-fixation model predictions with empirical evidence of boreal (forests and peatlands) bryophyte–diazotroph N_2-fixation in response to five direct and indirect global change factors: elevated CO_2, N deposition, warming, precipitation, and light (via shading); and (3) propose future directions for better integrating model and empirical studies to provide more robust predictions. We focus on empirical evidence of bryophyte–diazotroph N_2-fixation because it is the largest known source of biological N_2-fixation in northern latitude ecosystems (DeLuca et al., 2002; Houseman et al., 2020; Lindo et al., 2013). Our comparisons will provide novel insight into potentially divergent outcomes between models and empirical evidence, and propose a suite of research priorities that allow effective collaboration between modelers and empiricists.

2 | BIOLOGICAL N_2-FIXATION IN EARTH SYSTEM MODELS

The necessity of including N in Earth system models was critically highlighted in the seminal work of Hungate et al. (2003), which demonstrated a wide discrepancy between predicted future N availability and the amount of N required for predicted plant C uptake in elevated CO_2 environments. Models that explicitly included N constraints on terrestrial C cycling subsequently emerged in the late 2000s (e.g., Thornton et al., 2007). Since then, coupled C-N models have demonstrated that predictions of terrestrial C storage decline by 37%–58% when including N constraints on plant productivity (Davies-Barnhard et al., 2020; Wieder, Cleveland, Smith, et al., 2015; Zaehle & Dalmonech, 2011). Biological N_2-fixation, which is the most important N input in terrestrial ecosystems (Galloway et al., 1995), consequently became integral to coupled C-N models.

Two basic principles guide the modeling of biological N_2-fixation. First, only a small proportion of plant species can facilitate bacterial fixation of atmospheric N, either by association with epiphytic diazotrophs (nonvascular plants) or with the help of rhizobia or *Frankia* spp. residing in root nodules (vascular plants). Second, biological N_2-fixation is considered to be expensive; the C cost is estimated to be about 9 g C per g N fixed (Gutschick, 1981). On the surface, these two principles justify evaluating the relationships between NPP or AET and biological N_2-fixation. High NPP may imply high demand for N but also the ability to cover expensive N_2-fixation, consequently offering a larger niche for N_2-fixing species. Likewise, high AET is conducive to high plant productivity, again implying high demand for N and the ability to afford expensive N_2-fixation. However, this proposed N_2-fixation/productivity relationship resolved in these regression-type model fixation schemes is less certain under global change scenarios. For example, high rates of reactive N deposition may promote NPP, and models that relate N_2-fixation to NPP may subsequently predict increasing N_2-fixation. Yet, N deposition may instead provide sufficient plant N via root uptake without requiring the expensive N_2-fixing pathway, thereby reducing the need for N_2-fixation. Furthermore, while elevated CO_2 is expected to increase N demand (Hungate et al., 2003; Luo et al., 2004), AET may not keep pace due to increasing water use efficiency (Wieder, Cleveland, Lawrence, et al., 2015; Wieder, Cleveland, Smith, et al., 2015).

2.1 | Previous conceptual modeling exercises

Models that aim to represent a mechanistic underpinning of N_2-fixation use concepts where N_2-fixation emerges following a plant need for nitrogen. A common feature among these models is the adjustment of N supply vs. demand, and hence we refer to these models as homeostatic-type models. Applications of these concepts show, for example, that N_2-fixing plants are able to persist in ecosystems due to N limitations, which, in turn, persist due to ecosystem N losses from pools that are unavailable to plants (e.g., loss of organic N during fire) (Menge et al., 2008). Modeling studies have further suggested that N_2-fixing plants can persist despite potential limitations, including additional C cost for N acquisition, higher N demand due to higher tissue N concentration, or other implicit competitive disadvantages (e.g., light; Vitousek & Field, 1999). Some homeostatic-type models include opportunity cost considerations (e.g., reduced photosynthesis if C is partitioned toward root growth) that have led to other model formulations of relative costs of N_2-fixation versus root uptake, with conceptually similar results (Fisher et al., 2010). These include competitive advantages of N_2-fixers and higher N_2-fixation early in primary succession after a biomass-reducing disturbance (e.g., grazing or fire), and reduced N_2-fixation under higher reactive N inputs into the system. Overall, a study by Meyerholt et al. (2020) demonstrated that the capacity for C sequestration under future warming increases in models that take into account this homeostatic response of N_2-fixation to plant N demand. Notably, the divergence among models in this study is largest in high latitudes, owing to contrasting outcomes when biological N_2-fixation is modeled as a function of NPP or AET (i.e., regression-type models) versus plant N demand (i.e., homeostatic-type models, Meyerholt et al., 2020).

2.2 | Other considerations: Temperature, micronutrients, and phosphorus

In addition to the regression-type approaches using NPP or AET as predictors, and the homeostatic models where plant N demand is the major driver, several other factors have been considered to further influence N_2-fixation in Earth system models. Among the global change factors, temperature may play a direct effect on biological N_2-fixation rates, because activity of the main enzyme (nitrogenase) responds positively to a temperature increase with an optimum temperature around 25°C (Houlton et al., 2008). Furthermore, micronutrients such as molybdenum may limit the production of nitrogenase (Barron et al., 2009). Phosphorus acquisition, in turn, may favor N_2-fixing plants, because phosphatase production relies on N supply (Houlton et al., 2008). In ecosystem models, temperature suppresses

N_2-fixation in high latitudes due to increasing N mineralization while N requirements for phosphatase have been suggested to favor increased N_2-fixation in tropical ecosystems (Houlton et al., 2008).

2.3 | Current representation of N_2-fixation in models

None of the widely used Earth system models specifically considers boreal bryophyte–diazotroph N_2-fixation. Many current models correlate N_2-fixation with NPP or AET rates (Table 1), based on the study by Cleveland et al. (1999), who showed that these factors were correlated globally across biomes. Of the five terrestrial models in the Coupled Model Intercomparison Project 6 (CMIP6) that explicitly include N_2-fixation, JSBACH (Goll et al., 2017; Mauritsen et al., 2019), and JULES-CN (Wiltshire et al., 2020) model N_2-fixation as a positive function of NPP (linearly and nonlinearly, respectively). A third, the CABLE-CASACNP model (Wang & Houlton, 2009; Wang et al., 2010), separately predicts symbiotic and asymbiotic (primarily free-living N_2-fixers, including soil) N_2-fixation using a homeostatic approach and AET, respectively. The fourth model in CMIP6, LPJ-GUESS (Smith et al., 2014), includes N_2-fixation as a linear function of AET, again based on relationships in Cleveland et al. (1999). The fifth model, CLM5 (Lawrence et al., 2019), differentiates symbiotic from asymbiotic N_2-fixation: symbiotic N_2-fixation is included as a function of associated C costs (determined by soil temperature) based on the Fixation and Uptake of Nitrogen (FUN) model (Fisher et al., 2010; Lawrence et al., 2019), while asymbiotic N_2-fixation is predicted by a linear relationship with AET based on relationships in Cleveland et al. (1999). Although CLM5 and CABLE-CASACNP still predict asymbiotic N_2-fixation using a correlation with AET, the differentiation from symbiotic N_2-fixation represents an important step toward improved predictions of global N_2-fixation. However, many models still acknowledge considerable uncertainty in predictions of N_2-fixation in northern latitude regions (Davies-Barnard et al., 2020; Meyerholt et al., 2016; Wieder, Cleveland, Lawrence, et al., 2015; Wiltshire et al., 2020).

3 | COMPARING MODEL PREDICTIONS WITH EMPIRICAL DATA ON BOREAL BRYOPHYTE–DIAZOTROPH N_2-FIXATION

Because bryophyte–diazotroph N_2-fixation is the largest known source of biological N_2-fixation in northern latitude ecosystems (DeLuca et al., 2002; Houseman et al., 2020; Lindo et al., 2013), understanding its response to global change factors is critical for predicting future N cycling. The past decade has seen rapidly growing research into global change factors that could more accurately predict bryophyte–diazotroph N_2-fixation in northern latitude ecosystems when compared to NPP or AET. Elevated atmospheric CO_2, N deposition, warming, and altered precipitation regimes comprise four primary factors that have been shown to affect

TABLE 1 The nine Earth system models used in this study

Model	N_2-fixation type	N_2-fixation link	N_2-fixation reference	Model reference
JSBACH	No distinction	NPP	Cleveland et al. (1999)	Goll et al. (2017); Mauritsen et al. (2019)
JULES-CN	No distinction	NPP	Cleveland et al. (1999)	Wiltshire et al. (2020)
CABLE-CASACNP	Asymbiotic and symbiotic	Asymbiotic: AET symbiotic: C cost, temperature, nutrients, light	Cleveland et al. (1999) Wang et al. (2007); Houlton et al. (2008)	Wang et al. (2010); Wang and Houlton (2009)
LPJ-GUESS	No distinction	AET	Cleveland et al. (1999)	Smith et al. (2014)
CLM5	Asymbiotic and symbiotic	Asymbiotic: AET symbiotic: C cost and temperature, according to FUN model	Cleveland et al. (1999) Fisher et al. (2010)	Lawrence et al. (2019)
CLM4.5bgc	No distinction	NPP	Cleveland et al. (1999)	Oleson et al. (2010)
OC-N	No distinction	AET	Cleveland et al. (1999)	Zaehle and Friend (2010)
LM3V-N	Symbiotic	NDS (plant N demand and light limitation)	Gerber et al. (2010)	Gerber et al. (2010)
ISAM	No distinction	AET	Cleveland et al. (1999)	Jain et al. (2009)

Note: Further details of model parameters are found in Table S3.

Abbreviations: AET, actual evapotranspiration; NPP, net primary productivity.

bryophyte–diazotroph N_2-fixation. Ground-layer light availability, as a function of shading by higher vascular plant productivity, represents a secondary indirect factor that responds to global change and may, in turn, influence bryophyte–diazotroph N_2-fixation. Although some of these five factors are better studied than others, accounting for their effect on bryophyte–diazotroph N_2-fixation may help improve the representation of N_2-fixation in Earth system models.

To assess empirical findings of bryophyte–diazotroph N_2-fixation responses to five global change factors, we retrieved empirical N_2-fixation data published before January 2021 from the Web of Science database with a selection criterion including several keywords: moss or bryophyte or pleurozium or hylocomium or sphagnum; fixation; CO_2 or deposition or warming or moisture or precipitation or water or light or shade; boreal. Studies with confounding factors were removed, owing to the difficulty of ascribing effects to relevant global change factors. This criterion produced 20 studies with 80 treatment results (i.e., some studies had multiple treatment levels), with the number of treatment results per study (i.e., levels) ranging from 1 to 15. We standardized results by calculating the percent change in N_2-fixation and the percent change in N_2-fixation per treatment unit (Tables S1 and S2).

We then compared empirical findings to modeled changes in overall biological N_2-fixation using nine different Earth system models (Table 1). We chose these nine models because they (1) have published results of N_2-fixation in response to global change factors and (2) separated out boreal regions in the respective publication. These models employ various predictors of N_2-fixation, including NPP (Cleveland et al., 1999); AET (Cleveland et al., 1999); resource optimization (Rastetter et al., 2001); resource optimization with temperature-dependent adjustment (Houlton et al., 2008), carbon cost of N uptake (Fisher et al., 2010), carbon cost of N uptake with temperature-dependent adjustment (Fisher et al., 2010; Houlton et al., 2008), plant N demand and light limitation (Gerber et al., 2010), or a spatially variable but temporally constant rate. Several models differentiate asymbiotic N_2-fixation (i.e., nonvascular, primarily free-living soil N_2-fixers) from symbiotic N_2-fixation (i.e., vascular, Table 1). However, none of these models specifically considers boreal bryophyte–diazotroph N_2-fixation. For the purpose of this review, we grouped models into regression-type or homeostatic-type N_2-fixation schemes. Regression-type schemes include those that scale N_2-fixation directly with NPP and AET, whereas homeostatic-type models include formulations that respond more directly to N supply and demand via some form of homeostatic adjustment. We recognize that even models that include a C expenditure for N uptake might fail to adequately account for bryophyte–diazotroph N_2-fixing niches, which may or may not involve a direct C and N exchange (Stuart et al., 2020). We standardized the model results based on individual global change factors (i.e., "single forcing"). In cases of multiple factors combined (i.e., "multiple forcing," which always included mostly historic or future global change scenarios under CO_2 increase), we expressed N_2-fixation as a function of CO_2 increase. We further divided the modeling results into global or boreal, when publications separated out biomes or latitudes in individual results. Numbers were inferred from line graphs via Adobe Acrobat Reader distance tool. We broadly refer to boreal systems where investigators referred to "high latitude," "evergreen needle leaf plant functional type," or "boreal." Individual model results and citations are summarized in Table S3. Lastly, we do not consider interactions of factors in this study; although nonlinear responses are to be expected (e.g., Gerber et al., 2013), more research is needed to accurately determine the nature of potentially nonlinear responses.

3.1 | Elevated CO_2

The relationship between atmospheric CO_2 concentrations on bryophyte–diazotroph N_2-fixation has been the least studied global change factor. Elevated CO_2 could cause an increase in photosynthesis in both bryophytes and diazotrophs (Lindo & Griffith, 2017; Turetsky, 2003), such as it does for vascular plants, thus potentially increasing energy stores available for N_2-fixation. On the other hand, elevated CO_2 could indirectly decrease N_2-fixation by augmenting the growth of surrounding plants that consequently shade bryophytes, therefore lowering temperatures and reducing rates of photosynthesis, and ultimately lowering energy stores available for N_2-fixation (Gundale, Nilsson, et al., 2012; Sorensen et al., 2012). Moreover, the response of N_2-fixation to elevated CO_2 may depend on the availability of phosphorus, potassium, and molybdenum (Edwards et al., 2006; Hungate et al., 2004; Niklaus et al., 1998; Van Groenigen et al., 2006).

Empirical data from the single known relevant study demonstrate that a bryophyte-associated diazotroph (*Nostoc punctiforme*) has higher N_2-fixation rates under elevated CO_2 in culture, but this could depend on air temperature and the diazotroph growth stage (Lindo & Griffith, 2017; Table 2a). Lindo and Griffith (2017) found that N_2-fixation rates of cultured diazotrophs increased by a median of 0.09% for each 1 ppm CO_2 increase over 430 ppm (Table 2a; Figures 1 and 2). Specifically, N_2-fixation rates were 29.8% higher in 750 ppm CO_2 treatments compared to 430 ppm treatments, when averaged across warming treatments and time periods (Table S1). The effect was more consistent at 11.5°C when compared to 15.5 or 19.5°C, and was also stronger during the early exponential diazotroph growth period when compared to later time periods (Table S2), suggesting that CO_2 fertilization effects on N_2-fixation are context-dependent. Additional empirical data, particularly data from studies where diazotrophs live in association with bryophytes (which could produce different responses than when grown in culture), will be essential for inferring broad trends of elevated CO_2 effects on bryophyte–diazotroph N_2-fixation. However, we found that these limited empirical results were generally consistent with model predictions (Table 2; Figure 1). N_2-fixation in global and boreal Earth system models responded mostly positively to elevated CO_2, with a higher median response in homeostatic-type models (0.19%/ppm and 0.27%/ppm, respectively, Table 2b). Compared to boreal homeostatic-type models, boreal regression-type models (median of 0.05%/ppm) are more consistent with the single empirical study.

TABLE 2 Summary of (a) empirical studies that tested global change factors on boreal bryophyte–diazotroph N_2-fixation and (b) modeled response of N_2-fixation to global change factors (C: CO_2, T: climate, N: N deposition, or combinations thereof), globally and in boreal region

			N_2-fixation change (%) per factor unit				
Factor	**Treatment**	**Unit**	**Median**	**Average**	**Minimum**	**Maximum**	***n***
(a)							
CO_2	Addition	ppm	0.09	0.09	0.09	0.09	1
N deposition	Addition	kg N ha^{-1} year^{-1}	−4.50	−18.23	−110.74	32.63	36
		µg N g^{-1} soil dry weight	−111.35	−137.37	−275.21	19.31	5
		ml NH_4NO_3 g^{-1} moss dry weight	−3.06	−3.06	−3.06	−3.06	1
Warming	Addition	°C	24.77	20.66	−12.94	46.08	23
Precipitation	Addition	mm month^{-1}	0.30	0.30	0.30	0.30	1
Precipitation	Reduction	Actual % of days watered	−0.02	0.08	−0.66	1.20	8
		Actual % of total ambient precipitation over 4 years	−0.05	−0.05	−0.09	−0.0006	2
		mm month^{-1}	−1.39	−1.39	−1.39	−1.39	1
Light	Addition	µmol m^{-2} s^{-1}	0.26	0.26	0.26	0.26	2

			Regression-type					Homeostatic-type				
			N_2-fixation change (%) per factor unit					N_2-fixation change (%) per factor unit				
Scale	**Factor**	**Unit**	**Median**	**Average**	**Minimum**	**Maximum**	***n***	**Median**	**Average**	**Minimum**	**Maximum**	***n***
(b)												
Global	CTN	ppm	0.08	0.09	0.02	0.18	4	0.12	0.30	0.12	0.58	5
	CT	ppm	0.00	0.01	0.00	0.03	3	—	—	—	—	—
	C	ppm	0.03	0.05	−0.01	0.16	6	0.19	0.26	0.03	0.63	4
	T	K	−1.45	−1.45	−1.45	−1.45	1	—	—	—	—	—
	N	kg N ha^{-1} year^{-1}	0.20	0.16	0.02	0.20	4	−1.02	−1.02	−1.02	−1.02	1
Boreal	CTN	ppm	0.07	0.07	0.04	0.11	2	0.20	0.19	0.07	0.28	4
	CT	ppm	—	—	—	—	—	—	—	—	—	—
	C	ppm	0.05	0.06	0.01	0.15	4	0.27	0.27	0.27	0.27	1
	T	K	—	—	—	—	—	—	—	—	—	—
	N	kg N ha^{-1} year^{-1}	0.08	−0.12	−0.86	0.22	4	−0.94	−0.94	−0.94	−0.94	1

Note: Model responses are grouped into regression-type models that consider regression functions to net primary productivity (NPP) or actual evapotranspiration (AET), or homeostatic-type models that consider upregulation based on plant N deficits (see also main text). N, nitrogen; *n*, sample size. Further details for empirical studies (e.g., N_2-fixation measurement methods) and model studies are located in supplementary tables.

Global regression-type models predict a smaller median increase of 0.03%/ppm. Overall, the modeled responses to elevated CO_2 exhibit high variation, especially among the global homeostatic-type models.

3.2 | N deposition

Diazotroph N_2-fixation is downregulated when fixed N or other accessible forms of N (e.g., amino acids) are readily available (Fay, 1992). Consequently, there is ample evidence to demonstrate that N deposition negatively affects N_2-fixation. Among studies that assessed N deposition effects on bryophyte–diazotroph N_2-fixation in boreal ecosystems, we found that N_2-fixation declines by a median of 4.5% per 1 kg N ha^{-1} year^{-1} addition (Table 2a; Figures 1 and 2). Moreover, increases of up to 5 kg N ha^{-1} year^{-1} resulted in a median decline in N_2-fixation rates by 33.1%, ranging from −110.7% to +32.6% (Table S2), and N additions of 5–50 kg ha^{-1} year^{-1} also corresponded to a 2.8% median decline in N_2-fixation rates, ranging from −17.3% to +4.4% per 1 kg N ha^{-1} year^{-1} addition (Table S2). Although studies of boreal N deposition are limited to Fennoscandia, we expect similar trends of N_2-fixation rates in other northern latitude regions due to the known mechanisms that link N availability to diazotroph N_2-fixation.

Compared to empirical studies, homeostatic-type models predict more gradual rates of declining N_2-fixation under increased N deposition, while regression-type models predicted gradual increases in N_2-fixation under increased N deposition (Table 2b; Figure 1). Specifically, homeostatic-type models predict that boreal and global N_2-fixation declines by a median of 0.94% and 1.02%, respectively,

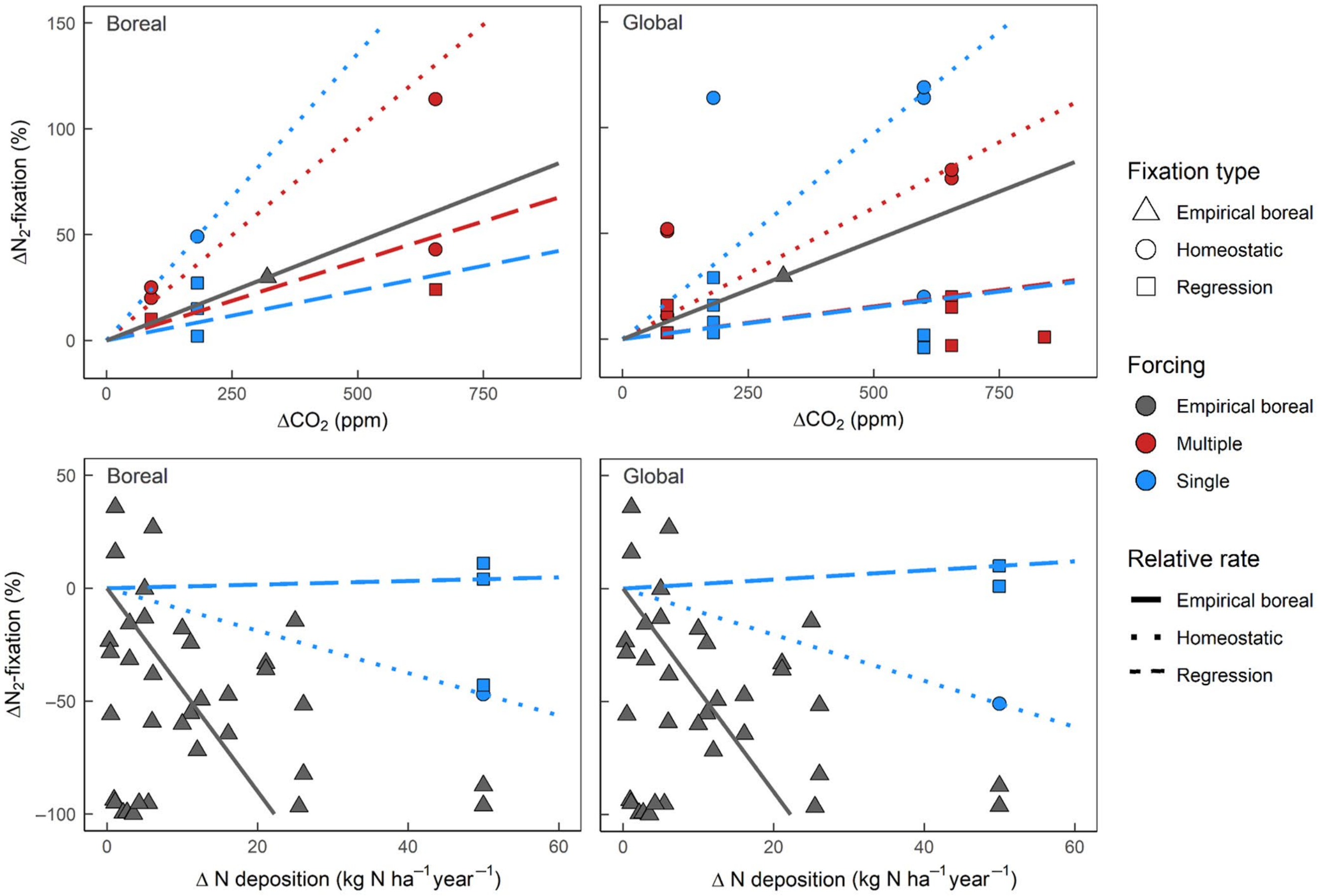

FIGURE 1 N_2-fixation change (%) in response to increasing CO_2 or N deposition among empirical and model studies. Empirical results represent median values from compiled bryophyte–diazotroph N_2-fixation studies in boreal ecosystems. Model results represent regional or global integrations. Regression-type models represent N_2-fixation based on net primary productivity (NPP) or actual evapotranspiration (AET), while homeostatic-type models bin the various adjustment schemes. Further details for empirical studies (e.g., N_2-fixation measurement methods) and model studies (e.g., parameterization) are located in supplementary tables

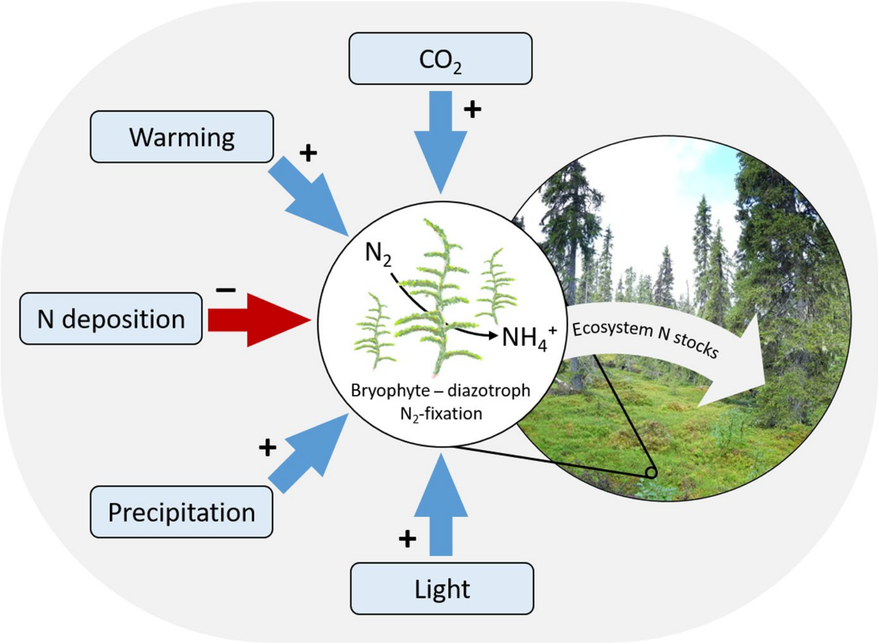

FIGURE 2 Conceptual diagram illustrating direct drivers of bryophyte–diazotroph N_2-fixation in boreal ecosystems from empirical studies. Blue arrows indicate positive effects; red arrows indicate negative effects. N, nitrogen. Photo credit: Paul Kardol

with each additional 1 kg N ha^{-1} year^{-1}, a rate far less than that found in empirical studies. In contrast, regression-type models predict that boreal and global N_2-fixation increase by a median of 0.08% and 0.20%, respectively, with each additional 1 kg N ha^{-1} year^{-1} (Table 2b; Figure 1.) While N deposition may increase vascular plant productivity, nearly all empirical studies found a decline in bryophyte–diazotroph N_2-fixation, regardless of the quantity of added N. Consequently, most models (including homeostatic-type models) overestimate N_2-fixation in N deposition scenarios, which could generate overestimations of future N stocks in boreal ecosystems unless other N_2-fixing niches (or higher N mineralization) compensate for declining bryophyte–diazotroph N_2-fixation. Overall, our synthesis of N deposition studies suggests that boreal N_2-fixation should not be scaled with NPP or AET.

3.3 | Warming

Warming may have several direct and indirect effects that could influence bryophyte–diazotroph N_2-fixation. The optimum temperature for nitrogenase reactions is near 25°C, beyond which N_2-fixation will theoretically decline (Houlton et al., 2008; Vitousek et al., 2002). This suggests a direct positive effect of warming on N_2-fixation in most northern latitude environments due to low yearly average temperatures, but other interacting factors resulting from warmer temperatures may indirectly weaken the response. First, warmer temperatures without concurrent increases in water availability may decrease bryophyte moisture content and thus negatively affect N_2-fixation, owing to lower diazotroph activity during dry periods (Gundale et al., 2009; Rajeev et al., 2013; Tracy et al., 2010), even after rewetting (Rousk et al., 2014b). Moreover, shifts in diazotroph community composition in response to warming could mediate declining N_2-fixation, though evidence for this is so far limited to *Sphagnum* (Carrell et al., 2019). Second, warming will likely increase vascular plant productivity, if only temporarily (Montgomery et al., 2020; Natali et al., 2012; Rice et al., 2018). This could increase competition for water and light, thus constraining N_2-fixation, but declining N availability due to heightened competition for nutrients could instead favor N_2-fixation. Third, warming may stimulate mineralization and consequently increase N availability (Hopkins et al., 2012; Xue et al., 2016), resulting in the downregulation of N_2-fixation and little overall change in N_2-fixation rates, as was found in a meta-analysis of arctic warming experiments (Salazar et al., 2020).

Among empirical studies that assessed temperature effects, we found that bryophyte–diazotroph N_2-fixation increased by a median of 24.8% for each 1°C increase in temperature (Table 2a; Figure 2). However, results often depended on study area, treatment, and bryophyte species. For example, one study found that the feather moss *Pleurozium schreberi* increased N_2-fixation by a median of 213.1% and 83.8% with warming of 5.7 and 14°C, respectively, above the 16.3°C control, suggesting that this species can increase N_2-fixation even beyond the proposed temperature optima (Gundale, Nilsson, et al., 2012; Table S2). Another feather moss, *Hylocomium splendens*, had smaller increases of 82.1% and 22.2% in 5.7 and 14°C warming, respectively. However, N_2-fixation of both species declined by up to 100% when warming was combined with high light (517.3 μmol m^{-2} sec^{-1}), suggesting that N_2-fixation can respond positively to warming, but not if high-light levels further increase foliar temperatures (Gundale, Nilsson, et al., 2012; Gundale, Wardle, et al., 2012, Table S2). In contrast with feathermoss, *Sphagnum fallax* N_2-fixation declined with increasing temperature in a whole-ecosystem peatland warming experiment, which the authors attributed to shifting composition of diazotroph communities as a possible response to lower soil moisture (Carrell et al., 2019). Clearly, more work is needed to test species-specific responses to warming (bryophyte-associated diazotroph species in addition to bryophyte species themselves).

Unfortunately, very few modeling studies exclusively test warming effects. The 2017 regression-type model study by Goll et al. suggests that warming decreases global N_2-fixation by 1.45% per 1°K warming (note that warming includes precipitation changes, Table 2b; Table S3), a finding which strongly contrasts with the median bryophyte–diazotroph N_2-fixation response of +24.8% per 1°C warming. We surmise that models with homeostatic-type N_2-fixation schemes would decrease under warming, given that the slope of N_2-fixation in response to multiple forcings (i.e., including warming) was lower than that of single forcing (i.e., excluding warming) under increasing CO_2 scenarios (Figure 1). Conceptually this makes sense, as elevated temperatures allow for enhanced N mineralization, and subsequently lower N demand and N_2-fixation. However, N_2-fixation may instead become more efficient under higher temperatures, as some models suggest. Ultimately, the wide discrepancy between model and empirical studies highlights the need for further investigation into warming effects on nonvascular N_2-fixation in boreal forests.

3.4 | Precipitation

Bryophyte moisture content often positively correlates with N_2-fixation owing to its positive effect on diazotroph growth and activity (Gundale et al., 2009; Turetsky, 2003). Moreover, nutrient leaching during precipitation events may be a crucial pathway through which N fixed by bryophyte–diazotrophs enters the soil N pool (Slate et al., 2019). Precipitation may consequently be an important driver of not only bryophyte–diazotroph N_2-fixation but also potential soil N. Among empirical studies that examined the link between boreal bryophyte–diazotroph N_2-fixation and water inputs, we found that increasing water input had positive effects on N_2-fixation, while reductions often had negative effects (Table 2a; Figure 2). However, the magnitude of change in N_2-fixation depended on treatment type. For example, watering every fourth day reduced N_2-fixation by a median of 15.5% when compared to daily watering (Table S2; Gundale et al., 2009), while decreasing water input from 60 to 20 mm month^{-1} reduced N_2-fixation by a median of 67.9% (Table S2; Jackson et al., 2011). Importantly, Gundale et al. (2009) found that bryophyte N_2-fixation from environments with higher soil moisture may be more sensitive to changes in precipitation when compared to that from environments with lower soil moisture, suggesting that models may need to account for site-specific differences. Taken together, available empirical evidence demonstrates a strong dependence of N_2-fixation on precipitation.

We could not find any modeling exercises with Earth system models that explicitly address precipitation responses of N_2-fixation. Conceptually, there are several pathways through which precipitation could affect N_2-fixation in models. In dry areas, plant N limitation can be enhanced as productivity increases; however, this may be countered (at least initially) by enhanced N mineralization. In homeostatic-type models, we expect a direct increase of N_2-fixation if water is limiting. However, modeling studies are needed to test these hypotheses, and may well be ecosystem-dependent.

3.5 | Light

The four global change factors described above could all promote vascular plant productivity and therefore increase shading of ground-dwelling N_2-fixing bryophytes (Montgomery et al., 2020; Natali et al., 2012). Nitrogenase reactions operate on energy produced by photosynthesis and consequently, decreased light availability could downregulate N_2-fixation. Among studies that manipulated light quantity, we found that bryophyte–diazotroph N_2-fixation increased by a median of 0.26% for each 1 $\mu mol\ m^{-2}\ s^{-1}$ increase in photosynthetically active radiation (Table 2; Figure 2). However, there is little evidence to confirm that light directly influences nitrogenase activity. Higher light intensity increases air and foliar temperature, which could also increase nitrogenase activity and therefore cause N_2-fixation rates to be higher if the resulting temperature remains below the ~25°C optimum (Gundale, Nilsson, et al., 2012; Sorensen et al., 2012). Although some models account for light requirements for vascular plant N_2-fixation to occur (e.g., Gerber et al., 2010), there are no published examples of models that exclusively manipulate light quantity to test the response of N_2-fixation, meaning that an empirical-model comparison is not possible at this time.

3.6 | Interactions among global change factors

Experimental work to assess the combined influence of all major global change factors (CO_2, N deposition, warming, precipitation, and shading) does not exist because of the logistical intractability of crossing all these factors in a single experiment. However, conceptual and quantitative models suggest that these factors have interactive effects on N cycling and N limitations, and therefore N_2-fixation. For example, elevated CO_2 would imply increased N limitation, but warming will offset N limitations by transiently increasing N mineralization and thus supporting N supply for growth. Enhanced N deposition could similarly alleviate N limitations caused by elevated CO_2. Earth system models predicting scenarios where CO_2, climate, and N deposition all change together predict that N_2-fixation will increase globally, with the fractional increase higher in boreal systems (Table 2b). The predicted increase is also higher in models with homeostatic-type N_2-fixation responses. Overall, the strongest modeled N_2-fixation effect appears to come from CO_2 while climate and N deposition tend to enhance N_2-fixation (in regression-type models) or reduce N_2-fixation (in homeostatic-type models) to some degree.

4 | CONSIDERING OTHER N_2-FIXING NICHES

Although bryophyte–diazotroph N_2-fixation is currently the largest known and most important source of biological N_2-fixation in northern latitude ecosystems (DeLuca et al., 2002; Lindo et al., 2013), global change could increase the abundance of some other N_2-fixing niches. For example, actinorhizal *Alnus* spp. can achieve very high N_2-fixation rates and typically colonizes flood plains or other riparian areas (Chapin et al., 2016; Houseman et al., 2020), and are often more abundant in deciduous forests than coniferous forests (Wurtz, 1995). Climate- or disturbance-driven shifts toward deciduous tree cover (Mack et al., 2021) could potentially promote the spread of *Alnus* spp. in some boreal regions (Houseman et al., 2020), and consequently increase stand-level N_2-fixation. However, the extent to which this could occur is unclear, given that *Alnus* spp. is restricted to moist soil conditions. The abundance of N_2-fixing leguminous ground-layer herbs, such as *Lupinus* spp., may also be favored by warming and human activity (Hendrickson & Burgess, 1989; Vetter et al., 2018), but are generally limited to non-forested areas (but see Graham & Turkington, 2000). Overall, global change (including human disturbance) could ultimately increase the abundance of vascular N_2-fixing plants in some boreal ecosystems, but more work is needed to predict these potential community shifts.

Limited data suggest that free-living soil N_2-fixation may account for approximately 10%–15% of total N_2-fixation in boreal conifer forests (Houseman et al., 2020). However, the response of free-living N_2-fixation to global change is uncertain. Experimental evidence indicates that free-living N_2-fixation responds positively to elevated CO_2, but only when supplemented with other nutrients, such as phosphorus (Eisel et al., 1989; Hofmockel & Schlesinger, 2007). Furthermore, temperature and moisture generally have positive effects on free-living N_2-fixation (Hofmockel & Schlesinger, 2007; Reed et al., 2011), but future warming and precipitation patterns could affect phosphorus availability and therefore influence free-living N_2-fixation rates (Dynarski & Houlton, 2018). Lastly, recent evidence has revealed N_2-fixing abilities of conifer-associated foliar endophytes (Moyes et al., 2016; Padda et al., 2019), but the response to global change is unknown.

5 | FUTURE DIRECTIONS

This review highlights several areas in which to improve the integration of model and field experiments for predicting N_2-fixation under

TABLE 3 Recommendations for integrating model and empirical studies to improve predictions of N_2-fixation in Earth system models

Study type	Recommendation
Model	• Explicitly account for nonvascular N_2-fixation to reduce discrepancies between models and empirical studies. • Do not scale nonvascular N_2-fixation with net primary productivity (NPP) or actual evapotranspiration (AET), but include more directs drivers of nonvascular N_2-fixation such as temperature or ground-layer light availability. • Model simulations with step-like increases in driving factors to better mimic field experiments.
Empirical	• New experiments to test global change effects on nonvascular N_2-fixation under scenarios lacking empirical data, such as CO_2,shading, and interactions. • Measure other important variables such as N mineralization, plant growth, and strength of existing N limitations. • Report site history (e.g., land-use history).

global change scenarios (Table 3). First, our findings demonstrate that models should explicitly consider nonvascular N_2-fixation, especially in high latitude ecosystems where nonvascular N_2-fixation is the largest known biological N input (DeLuca et al., 2002; Gundale et al., 2011; Jean et al., 2012; Houseman et al., 2020). Currently, few models account for nonvascular (including free-living) N_2-fixation, and if they do, use regression relationships with NPP or AET. We found that the direction of the relative response (percent change) broadly agreed with homeostatic model schemes used for vascular plants, but less with regression-type schemes. This suggests that future nonvascular N_2-fixation in models may include responses to N supply vs. demand considerations. Our analysis also indicates that the relative response to N deposition is under-predicted in models compared to empirical data, which may be partly explained by the location of the resource pools. In models, vascular plants have access to soil and water but nonvascular N_2-fixers may have limited access to soil resources, a differentiation that should be reflected in future models of nonvascular N_2-fixation. Furthermore, absolute growth rate and associated N demand are likely much smaller in nonvascular plants, which would augment effects of N deposition on the relative change in N_2-fixation through steeper downregulation.

Second, while homeostatic models are generally more conceptually sound than regression-type models, the spread in models is unsatisfying and may carry through to any implementation and prediction for nonvascular N_2-fixation. A focus on more direct forcing effects on nonvascular N_2-fixation (e.g., CO_2, N deposition, warming, precipitation, and vascular plant productivity) may help better parameterize the models and reduce model spread. Comparison with field experiments that intentionally manipulate abiotic drivers may provide a good starting point. Third, model simulations could likewise better mimic field experiments through step increases in driving variables, as is typically done in empirical experiments. Although models evaluate responses using realistic future scenarios, incorporating step changes of individual global change factors would allow easier comparison between model predictions and empirical findings.

Our analysis also suggests that field experiments could be better tailored to improve Earth system models. First, there is currently almost no empirical data describing the effect of CO_2 or shading on nonvascular N_2-fixation, indicating a strong demand for field experiments on these factors to make stronger comparisons with models. Moreover, most models do not isolate individual climate factors, but rather use the interactions of several factors (e.g., warming × elevated CO_2 × precipitation) to test realistic future scenarios. Field experiments should likewise test similar climatic interactions to better inform modeling efforts. Second, field experiments could better inform modeling efforts by measuring other important variables such as N mineralization, vascular and nonvascular plant growth, and the strength of existing N limitation (such as by measuring photosynthetic rates under ambient and elevated soil N availability), whose dynamics are determining factors in some land surface models. The response of N_2-fixation in homeostatic-type models is often linked to subtle changes in N supply and demand, and therefore hinges on the ability of the model to predict the larger N and C cycle. Third, it follows that site history is another important factor that would help improve homeostatic-type models, particularly because disturbances create shifts in N limitation and demand (Gerber et al., 2010; Rastetter et al., 2001). Field studies should consequently report as much site history as possible to accompany N_2-fixation results. In addition to integrating modeling and field studies, much work is needed to characterize the mechanistic nature of bryophyte–diazotroph associations to better predict N_2-fixation. Functional genomics and meta-transcriptomics approaches, such as those proposed by the Sphagnome Project (Weston et al., 2018), can help identify potential differences in bryophyte gene expression and microbiomes that regulate bryophyte–diazotroph N_2-fixation rates. For example, different microbiome communities and their unique responses to warming or seasonality may likewise drive *Sphagnum* and feathermoss N_2-fixation to respond differently to global change factors (Carell et al., 2019; Warshan et al., 2016). Identifying the environmental or site conditions that influence the bryophyte microbiome or gene expression could therefore improve model formulation and parameterization by specific characterization of microbiome traits.

6 | CONCLUSIONS

Overall, we found that Earth system models and empirical studies frequently agreed on the direction of change in N_2-fixation under elevated CO_2 and N deposition, in particular when the model scheme followed the homeostatic-type implementation. However, the magnitude of change under N deposition scenarios was much stronger in empirical studies, suggesting that models (and regression-type models in particular) may be overestimating boreal N_2-fixation in N deposition scenarios, and may be a result of different alternate pools of N sources (soil N or depositional N for vascular and nonvascular plants, respectively). Moreover, empirical findings of CO_2 effects are limited to a single study, highlighting a strong demand for more experimental work in this area. Under warming scenarios, models mostly predicted declining N_2-fixation while empirical studies usually found strongly increasing N_2-fixation. The discrepancy between models and empirical studies under warming scenarios could be the result of models that predict higher N mineralization under warming, and consequently, reduced demand for fixed N from vascular N_2-fixing plants. Data from long-term empirical studies are needed to confirm these model predictions while modeling studies that focus on boreal ecosystems and nonvascular N_2-fixation are needed to determine if N_2-fixation in boreal ecosystems accurately reflects global trends under warming scenarios. Precipitation and light have yet to be exclusively manipulated in models but we found overall positive effects of both factors on N_2-fixation in empirical studies. Ultimately, we recommend that models better represent the dynamics of nonvascular N_2-fixation, and that field studies include more targeted measurements to test model formulations and parameters. Though nonvascular N_2-fixation is relatively low when compared to vascular N_2-fixation on a global scale, it remains by far the largest known input of N in high latitudes (i.e., boreal and arctic ecosystems), which indicates much more attention should be paid to how it is represented in Earth system models.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No new data were generated for this study. All data and associated references are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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