Fire, climate and biotic interactions shape diversity patterns along an Afrotropical elevation gradient

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Abstract
Aim: Untangling multiple drivers influencing biodiversity along elevation gradients is necessary for predicting the consequences of climate change on mountain communities. We examine the direct and indirect effects of macroclimate, edaphic conditions, fire frequency and putative biotic interactions on species richness and abundance of co-occurring primary producers on Mount Cameroon.

Location: Mount Cameroon, Cameroon.

Taxon: vascular plants, bryophytes and lichens, and soil microbial phototrophs.

Methods: We combine ground-level survey of multi-taxon diversity, soil nutrient stoichiometry, continuous climate monitoring using dataloggers and remote sensing data, for 115 plots sampled along a 2200–4000 m elevation gradient. We used GAMs to assess elevational patterns in ecosystem properties and SEMs to determine their direct and indirect effects on species richness and abundance.

Results: Vascular plant diversity peaked at mid-elevation and emerged from the combined effects of intermediate levels of energy, total above-ground standing biomass, fire frequency, guild abundances and edaphic conditions. Bryophyte–lichen diversity increased monotonically towards high elevation with decreasing temperature and increasing nutrient scarcity, while the diversity of soil phototrophs peaked at both lower elevation fire-prone Afromontane and cold higher elevation Afroalpine zones. The role of macroclimate was indirect and scale dependent. Higher temperatures increased plant richness mainly indirectly via enhanced fire frequency, while soil N:P ratio had direct positive effect on plant richness. Precipitation decreased plant richness indirectly via decreased fire frequency. Fires also increased plant and bryophyte–lichen cover. Positive bryophyte–lichen and vascular plants associations strengthened in the Afroalpine zone.

Main conclusions: We demonstrate the role of disturbance/fire and biotic interactions in mitigating macroclimate effects and in controlling variation in community diversity.
along elevation gradients. While the macroclimate is often a strong predictor of ecological patterns along elevation gradients, our study illustrates that attributing these patterns exclusively to climate can lead to an incorrect assessment of the impact of climate change on biodiversity.

**KEYWORDS**

biotic interactions, elevation gradient, fire disturbance, precipitation, scale, soil fertility, species richness, temperature

# 1 | INTRODUCTION

The growing rate of habitat and biodiversity loss has led to an increased interest in exploring the patterns and determinants of native species diversity (Brummitt et al., 2020), especially in ecosystems undergoing rapid environmental change, such as mountain systems (Lomolino, 2001; McCain & Grytnes, 2010; Nogués-Bravo et al., 2008; Rahbek, 1995; Rahbek et al., 2019). One of the most commonly observed patterns along elevation gradients in plants, the hump-shaped pattern with peak species richness at mid-elevation (McCain & Grytnes, 2010; Rahbek, 1995), often correlates strongly with climate variables (Field et al., 2009). The causality of this general relationship has direct implications for the management and conservation of mountain biodiversity in the context of climate change (Nogués-Bravo et al., 2008). However, two decades ago, Lomolino (2001) reviewed the idea that ‘general patterns in nature may result from the combined effects of many redundant, or convergent processes, rather than the presumed independent effects of one overriding force’ (Lomolino, 2001). Indeed, patterns of plant diversity usually emerge from the complex interplay of multiple environmental drivers, such as abiotic factors (e.g. climatic and edaphic conditions), biotic interactions (e.g. competition or facilitation) and disturbances (e.g. fire or grazing). Their respective roles in shaping diversity patterns have been extensively studied at various scales (i.e. grain and extent) and are still debated (Connell, 1978; Grime, 1973; Hacker & Gaines, 1997; Huston, 1979; McCain & Grytnes, 2010). However, less attention is paid to the interrelationship between these drivers and indirect effects (e.g. Grace et al., 2016; Veldhuis et al., 2016). This knowledge is necessary to make more accurate and realistic forecasts of the impacts of climate change on biodiversity.

Macroclimatic factors that determine energy and water availability significantly affect diversity patterns on a large scale (Field et al., 2009; Hawkins et al., 2003; McCain & Grytnes, 2010), or in communities along gradients (Bryant et al., 2008; Grace et al., 2016; Peters et al., 2016). Decreased vascular plant diversity is often associated with reduced growth and productivity due to cold, drought or heat while higher richness is found amid temperature and precipitation gradients (Field et al., 2009; Hawkins et al., 2003; Rahbek et al., 2019). Because macroclimate changes in a very predictable way along elevation gradients (Körner, 2003), and the distribution of species richness is not uniform along elevation, climate variables are often strong predictors of this pattern (McCain & Grytnes, 2010; Rahbek et al., 2019). This strong or even general relationship between patterns of species richness and climate variables does not necessarily imply that their effects are direct. First, this relationship appears to be sensitive to the scale of the study (Nogués-Bravo et al., 2008), and the primacy of climate variables tends to be weaker when the pattern is examined with fine grain and small extent (Field et al., 2009). Second, climate variables are rarely independent of other environmental factors, such as disturbances or edaphic conditions (Spehn et al., 2006 and references therein; Chauvier et al., 2021; Nogués-Bravo et al., 2008), and this is despite their prominent influence on the vertical distribution of vegetation belts, the occurrence and abundance of species and their specific adaptation along the elevation gradient (Körner, 2003; Liancourt et al., 2020). For instance, high temperatures and associated water deficits cause regular fires, which is itself one of the drivers of plant diversity (Lehmann et al., 2014; Pausas & Ribeiro, 2017). The importance of fire to mountain biodiversity in tropical areas is well documented (Spehn et al., 2006 and references therein). Similarly, grazing and land use in general are also strongly associated with elevation (Chauvier et al., 2021; Nogués-Bravo et al., 2008; Spehn et al., 2006; Wesche et al., 2000). Omitting the key role of disturbance, edaphic conditions and scale could provide erroneous predictions about the effects of energy and water availability on diversity patterns (Field et al., 2009).

Finally, diversity patterns and their drivers often differ between the various guilds of co-occurring primary producers (Bruun et al., 2006; Bryant et al., 2008; Di Nuzzo et al., 2021; Grau et al., 2007; Peters et al., 2016), such as vascular plants (e.g. grasses, forbs, legumes, etc.), non-vascular cryptogams (e.g. bryophytes and lichens) or soil microbial phototrophs (cyanobacteria and algae). These differences are commonly attributed to their contrasting demand for energy and water availability (e.g. Grau et al., 2007). Like vascular plants, non-vascular terrestrial cryptogams and soil phototrophs, key components of biological soil crusts, are climate sensitive (Baldauf et al., 2021; Di Nuzzo et al., 2021; Rodriguez-Caballero et al., 2018). Yet, they are also susceptible to disturbance such as fire (Palmer et al., 2020), and the impact of climate variables on their diversity patterns could be indirect. Moreover, different guilds of primary producers are often considered independently of each other (e.g. Bruun et al., 2006; Bryant et al., 2008; Grau et al., 2007; Peters et al., 2016) or merged into one group (e.g. Peters et al., 2016). However, bryophytes, lichens and soil phototrophs alter
edaphic conditions (soil stability, water availability, nutrient fixation; Rodríguez-Caballero et al., 2018) and interact with vascular plants (competition and facilitation, Freestone, 2006; Bruun et al., 2006; Gavini et al., 2019), and although they are likely to contribute to the species richness patterns in vascular plants (Rehakova et al., 2017), their influence is rarely considered.

Tropical mountains in western Cameroon have been identified as biodiversity hotspots with extraordinary species diversity (Maicher et al., 2020). Afrotropical and Afroalpine ecosystems in Cameroonians Mounts provide unique opportunities to explore the guild interaction patterns across disturbance and resource availability gradients due to periodic fires and contrasting thermal and hydrological conditions that change predictably with increasing elevation (Hall, 1973; Keay, 1955). Different disturbance agents, such as regular fires in warmer lower elevations or erosive processes in colder higher elevations, together with biological fixation of nitrogen by cyanobacteria and legumes, can significantly affect the stoichiometry of nitrogen and phosphorus in the soil and thus the composition and structure of plant communities (Körner, 2003; Palmer et al., 2020; Rehakova et al., 2017; Rodríguez-Caballero et al., 2018).

The objectives of our study were threefold: (1) We evaluated the effects of climatic constraints, resource limitation (N:P ratio), fire frequency and putative biotic interactions on the richness and abundance of vascular plants (and their main functional groups), bryophytes–lichens and soil microbial phototrophs (cyanobacteria and algae). We used general additive models (GAMs) to assess these effects across the complete 2200–4000 m elevation range of Afrotropical and Afroalpine vegetation on Mount Cameroon, West Africa. We expected vascular plant diversity to peak at mid-elevation, not only because of climate, but also due to intermediate levels of resource availability, fire disturbance, and a more even representation of competing guilds and their main functional groups, in line with long-standing hypotheses (Connell, 1978; Grime, 1973; Huston, 1979). We also expected that two other guilds of primary producers, bryophytes–lichens and soil microbial phototrophs, would show a different pattern of variation along the elevation gradient due to their different response to abiotic and biotic drivers (Bruun et al., 2006; Bryant et al., 2008; Di Nuzzo et al., 2021; Grau et al., 2007; Peters et al., 2016). (2) We disentangled the direct and indirect effects of the abiotic and biotic factors on diversity patterns using structural equation modelling (SEMs). Our hypothetical causal model was inspired by a theoretical relationship proposed by Lehmann et al. (2014) between macroclimate variables, soil fertility and fire, to which we added relations between guilds. Our fundamental expectation was that diversity patterns would emerge from the complex interplay of these multiple factors. In particular, we expected that the effect of macroclimate could be largely indirect. (3) Finally, to assess the system and the scale specificity of our findings (Field et al., 2009), we compared the difference in the respective role of the abiotic and biotic drivers between the entire gradient and two distinct Afrotropical and Afroalpine zones, where we expected that different direct and indirect effects could affect variation in species richness.

2 MATERIALS AND METHODS

2.1 Study area

This study was conducted on the southwestern slopes of Mount Cameroon (4040 m a.s.l.), the highest mountain in sub-Saharan West and Central Africa (Figure 1a). The study area is located in the Mount Cameroon National Park, in a perhumid tropical climate that is essentially influenced by alternating southwestern maritime winds (monsoon) and northeastern continental dry winds (harmattan). Significant seasonality consists of one wet season (June–September) and one dry season (end of December–February), separated by relatively short transition periods (Hall, 1973). In the lowlands of the mountain, an average of 11 m of rain falls per year, making it one of the wettest places on Earth. Mount Cameroon is forested to c. 2200 m a.s.l. Above this elevation, the vegetation is first formed by large areas of fire-prone savanna-like grasslands, the Afromontane zone (Figure 1c), dominated by tall tussock plants of savanna genera such as Loudetia and Andropogon (C4 photosynthetic pathway). This savanna-like vegetation is considered a fire-degraded derivative of the mountain woodland, where trees are largely confined to protected gulleys (Hall, 1973; Keay, 1955). At higher elevation (Figure 1b), it gives way to the Afroalpine zone, shorter vegetation dominated by genera of temperate region affinity (C3 photosynthetic pathway, for example, Festuca, Deschampsia, Koeleria, Silene) (Hall, 1973; Keay, 1955). The study area is under local protection and human activity in these two zones is quasi-absent, with the complete absence of livestock grazing in the study area. Fire is of natural origin and grazing by wild ungulate is generally low (Hall, 1973).

Species richness and abundance of vascular plants, bryophytes, lichens, soil phototrophs and physicochemical parameters were recorded in the Afromontane and Afroalpine zones on 115 4 × 4 m plots placed at approximately 80–100 intervals from the forest boundary to the summit (Table S1, Figures S1–S6).

2.2 Climate data

Mount Cameroon weather stations are scarce and no station operates above 1000 m a.s.l. To assess the impact of climatic variables on diversity changes, we obtained monthly datasets of five climatic variables for each plot for the period 2000–2014 from the TerraClimate database (Abatzoglou et al., 2018; spatial resolution 1/24 degrees; Table S1) and calculated mean annual values of maximum temperature, precipitation, radiation, vapour pressure deficit (VPD) and Palmer Drought Severity Index (PDSI). To verify that the gridded data met local conditions at Mount Cameroon, we recorded the in-situ air temperature (+10 cm above-ground) in 15-min intervals using seven TMS loggers (Wild et al., 2019) located from the forest boundary to the summit in approximately 300 intervals (see Figure 1). Precipitation was recorded using seven rain gauges (EMS, Brno, Czechia), which were regularly cleared of vegetation to prevent fire damage and rainfall interception by vegetation. Gridded temperature and precipitation data were highly correlated \( r = 0.75–0.99 \) with our instrumental records and therefore represent a reliable source of information for examining
the relationships between climate variables and diversity patterns. Our subsequent analyses, therefore, use TerraClimate data. The average fire density for the period 1997–2010 was obtained for each plot from the Global Risk Data Platform based on the modified algorithm 1 product of the World Fire Atlas (WFA, ESA-ESRIN) dataset. The unit is the expected average number of events per 0.1 decimal degree pixel per year multiplied by 100 (e.g. 64 value means 0.64 events per year).

2.3 | Soil physicochemical characterization

To characterize soil nutrients, 150 g of soil was taken from each plot as a composite of 5 subsamples of soil (1–5 cm deep). The samples were oven-dried at 100°C, ground in a mortar and sieved to a 2-mm fraction after removing the roots. The major cations (Ca$^{2+}$, Mg$^{2+}$, K$^+$, and Na$^+$), as well as total nitrogen and phosphorus, were measured in all soil samples. Cations were quantified by atomic absorption spectroscopy (AAS) using SpectrAA 640 (Varian Techtron). Total nitrogen was determined colorimetrically after Kjeldahl mineralization using a FIAstar 5010 Analyser. Plant available phosphorus was determined colorimetrically after digestion in HClO$_4$ using a SHIMADZU UV–1650PC spectrophotometer. Other physicochemical data were also measured: pH (soil/water 1:5 w/v), soil organic matter content (SOM dry combustion at 450°C for 5 h) and texture (wet sieving, the percentage content of particles >0.5 mm in diameter, higher fractions indicate coarser soils). We used soil stoichiometric nutrient ratios in combination with nutrient concentrations to identify whether plant diversity is related to N, P and K limitations (see Table S1 for the list of variables measured).

2.4 | Taxonomical composition of above-ground primary producers

We recorded the composition of vegetation by visual estimation of the cover of all vegetation layers (E3-trees, E2-shrubs, E1-herbs, E0-bryophytes and lichens) and individual species in each layer on each plot. The above-ground primary producers were considered to be two distinct groups, vascular plants and non-vascular cryptogams. Vascular plant species were divided into functional groups: graminoids (grasses, sedges, rushes), non-legume forbs, legume forbs and shrubs (hereafter legumes), non-legume shrubs and subshrubs (hereafter shrubs), and pteridophytes (lycophytes and ferns). Graminoids were further subdivided according to their C3 and C4 photosynthetic pathways. Non-vascular cryptogams were divided into bryophytes and lichens. An additional rationale for considering bryophytes and lichens within the same guild, beyond their lack of vascular structure, is that they are both rootless and slow-growing poikilohydric organisms more likely impacted by climate change than vascular plants (Di Nuzzo et al., 2021).

2.5 | Taxonomical composition of soil phototrophs and their biomass

The same soil samples used to characterize the physicochemical parameters were used to determine the biovolume, number of phototroph cells and taxonomical composition of soil phototrophic microbes (soil phototrophs). Phototrophic cell numbers and taxonomic composition were determined by light and epifluorescence
microscopy (Olympus BX 60). Blue and green excitation was used to identify and quantify eukaryotic algae and cyanobacteria, respectively (MWB filter cube blue excitation 450–480 nm, emission 515 nm + for eukaryotic algae; MWG filter cube green excitation 510–550 nm, emission 590 nm + for cyanobacteria) (see Rehakova et al., 2017). Cyanobacteria included various taxonomic and morphological groups: Chroococcales (single-celled organisms), Oscillatoriales (filamentous cyanobacteria without heterocysts and akinetes), Nostocales (two families were distinguished—Nostocaceae as filamentous or colonial cyanobacteria with heterocysts and akinetes, and Hapalosiphonaceae as filamentous cyanobacteria with akinetes and heterocysts, with true branching of filaments—both N-fixers unlike single-celled and filamentous cyanobacteria without heterocysts). Eukaryotic algae were presented here as diatoms and Chlorophyceae (mainly coccal morphotypes).

2.6 | Data analysis

To evaluate the bivariate relationships between elevation changes in climatic and soil physicochemical parameters, as well as the richness and abundance of the three guilds of primary producers and their functional groups, we fitted response curves using generalized additive models (GAM), using the R package ‘gam’ (Hastie, 2020), with quasi-Poisson, quasi-binomial or Gaussian distributions depending on the nature of the response variable (soil variables, species counts, percent cover, biovolume). The GAM framework is useful for discovering elevation-specific patterns, does not rely on any predefined relationships and provides easy-to-interpret visualizations (McCullagh & Nelder, 1989). To assess whether the elevation responses were linear or unimodal (humped or U-shaped), we compared the fit of the first- and second-order polynomials using the chi-square AIC score test and presented only the results of the best models.

We fitted a piecewise structural equation model (SEM), using the R package ‘piecewiseSEM’ (Lefcheck, 2016), to reveal the relationships between predictor variables (climate, fire frequency, soil properties) and response variables (guild richness and abundance), and to disentangle their direct and indirect effects. Prior to analyses, all variables were standardized by z-transformation. We formulated a hypothetical causal model, the initial full SEM, which included all hypothetically causal relationships between the considered factors, that is, temperature, precipitation, fire frequency, soil N:P ratio, plant cover, bryophyte–lichen cover, soil phototroph richness and vascular plant species richness (Figure S7). For instance, we assumed that temperature and precipitation affect species richness directly and indirectly via their combined effect on standing biomass (for which we used total vegetation cover as a proxy), soil nutrients, fire frequency (see also Lehmann et al., 2014) and on the abundance of two other guilds of primary producers (bryophytes–lichens and soil phototrophs). Mutual interactions between plant richness and cover and individual guilds were included as they can interact with each other. We proceeded in a standard model selection following a backward procedure and used AIC together with Fisher’s C statistic with p > 0.05 to assess the goodness-of-fit of SEM and to determine the final model. To test the sensitivity of our model to the spatial extent of the gradient, we first fitted the SEM for the entire elevation gradient (n = 115), and then separately for Afromontane (2200–3200 m, n = 60) and Afroalpine zone (3200–4000 m, n = 55), where we expected that distinct direct and indirect influences could affect variation in species richness.

3 | RESULTS

3.1 | Elevational changes in climatic and soil conditions

Irrespective of the shape of variation (linear, hump- or U-shaped), all measured environmental variables show a significant trend along the elevation gradient. Between the tree line and the summit of Mount Cameroon (Figure 2), the mean annual temperature decreased from 17 to 3°C (p < 0.001, Figure 2a), and mean annual precipitation varied from c. 2500 to 1100 mm (Figure 2b). Precipitation showed a U-shaped elevation pattern, with the lowest rainfall between 2600 and 3200 m (p < 0.001, Figure 2b). Fire frequency and vapour pressure deficit were highest at the lowest elevations and decreased significantly from the Afromontane to the Afroalpine zone (both p < 0.001, Figures 2c and S8). Soil organic matter, total nitrogen, pH, calcium and magnesium decreased with elevation, soil coarseness peaked at mid-elevations around 3000–3200 m, while phosphorus and potassium had the lowest values at mid-elevation and higher concentrations in the lower Afromontane and upper Afroalpine zones (in all cases p < 0.05, Figures 2 and S8). Both N:P and N:K ratios peaked at mid-elevation, while the K:P ratio steadily increased with elevation (p < 0.01, Figures 2 and S8).

3.2 | Elevational changes in vascular plants, bryophytes–lichens and soil phototrophs

The sampled vascular plant communities contained a total of 131 species from 98 genera and 45 families, including 118 flowering plants and 13 pteridophytes. The most species-rich families were Asteraceae (22 taxa), Poaceae (21), Lamiaceae (7), Fabaceae (5), Campanulaceae (4) and Orchidaceae (4). The most abundant species were Poaceae, which accounted for 63% of the total vegetation cover, followed by Fabaceae (11%), Asteraceae (6%), Lamiaceae (4%) and Ericaceae (4%). The species richness of vascular plants showed a hump-shaped elevation pattern (p < 0.001, Figure 2g), with a maximum diversity at around 3000–3200 m. In contrast to species richness, the total vegetation cover decreased steadily with elevation, from 90% to 30% on average (p < 0.001, Figure 2j).

The functional groups of vascular plants showed significant differences in their elevational richness and abundance patterns. C4 graminoids predominated in the Afromontane zone between 2200 and 2800 m (Figure S9a,b), where the legumes also had the
The richness of C3 graminoids steadily increased with elevation up to 3200 m and then decreased towards the summit ($p < 0.001$, Figure S9c). The cover of C3 graminoids increased with elevation and levelled off at around 3400 m ($p < 0.001$, Figure S9d). The richness of non-legume forbs decreased with elevation ($p < 0.001$, Figure S9g), while their cover showed a U-shaped elevation pattern with the lowest values at mid-elevation (Figure S9h). Thus, C3 graminoids and non-legume forbs predominated in the Afroalpine vegetation above 3400 m. Shrub richness and shrub cover peaked at mid-elevation ($p < 0.05$, Figure S9i). Pteridophytes richness significantly decreased with elevation ($p < 0.05$, Figure S9j). Pteridophyte cover decreased slightly with elevation, but this trend was insignificant.

We found 40 species of bryophytes and 15 species of lichens. Their total richness and cover grew linearly with elevation, from 2 to 7 species on average, and from 10% to 30% cover (both $p < 0.05$, Figures 2h,k and S9k,i). Soil phototrophs were found in 74% of the plots. The phototrophic communities contained 60 morphotypes: 43 cyanobacteria, the dominant component of the communities and 17 microalgae. The most diverse were the Chroococcales with 27 morphotypes, followed by green algae (12 morphotypes), Nostocaceae (7), Oscillatoriales (7), Diatoms (5) and Hapalosiphonaceae (2). In terms of biovolume, the most abundant order was Chroococcales (39% of total biovolume), followed by Nostocaceae (20%), Oscillatoriales (17%), Hapalosiphonaceae (15%), with microalgae being the least represented group. The species richness of soil phototrophs showed a U-shaped elevation pattern ($p < 0.01$, Figure 2i), with the lowest richness recorded between 2800 and 3400 m.
The total phototrophic biovolume increased steadily with elevation ($p < 0.05$, Figure 2). Oscillatoriales were most abundant in the Afromontane zone ($p < 0.01$, Figure S9o), while Chroococcales and Nostocaceae dominated in the Afroalpine zone (both $p < 0.05$, Figure S9m,n).

### 3.3 Relationships between species richness, abundance and soil nutrients

Significant bivariate relationships between richness and plant cover were observed in all three groups of primary producers (Figure S10). Plant richness and total plant cover showed a significant hump-shaped relationship ($p < 0.001$, Figure S10a), with a maximum richness of 45%–55% of plant cover. Both bryophyte–lichen richness and cover had a negative relationship to plant cover (both $p < 0.001$, Figure S10b,d). In contrast, the richness of soil phototrophs, as well as their biovolume, showed a U-shaped pattern with plant richness and cover (both $p < 0.01$, Figure S10c,e). In terms of associations with soil nutrient gradients, plant species richness correlated significantly and positively with soil N:P ratio ($r = 0.41$, $p < 0.001$), nitrogen ($r = 0.40$, $p < 0.01$) and calcium ($r = 0.46$, $p < 0.01$), and negatively with soil phosphorus ($r = -0.25$, $p < 0.05$).

### 3.4 Structural equation modelling results: Abiotic, biotic and disturbance effects

Structural equation modelling provided further evidence of climatic constraints and fire disturbances as key mechanisms driving species richness and plant cover variation through multiple direct and indirect effects. Overall, the model applied over the entire elevation gradient fit our data well (Fisher's $C = 0.265$, df = 2, $p = 0.876$; $n = 115$, Figure 3a).

In total, climate variables, fires frequency, soil properties and inter-guild interactions explained 37% of the variation in plant species richness, 45% of the variation in plant cover, 35% of the variation in bryophyte–lichen cover and 15% of the variation in the richness of soil phototrophs. The strongest positive effect on plant richness was from fire frequency (standardized path coefficient of direct effect $= 0.688$, $p < 0.05$) and indirectly from the
maximum temperature through increased fire frequency (indirect effect = 0.592, \( p < 0.001 \)). The soil N:P ratio and bryophyte–lichen cover also had a strong positive effect on plant richness (direct effects = 0.235 and 0.199, both \( p < 0.05 \)). Fires also had a direct positive effect on plant cover (direct effect = 0.730, \( p < 0.01 \)) and bryophyte–lichen cover (direct effect = 0.586, \( p < 0.01 \)), but there was a strong negative relationship between bryophyte–lichen and plant cover. Precipitation did not have a significant direct effect on plant richness but had a negative indirect effect by decreasing fire frequency (indirect effect = –0.269, \( p < 0.05 \)). Precipitation also directly increased the richness of soil phototrophs (direct effect = 0.461, \( p < 0.001 \)).

Separate analyses for Afromontane and Afroalpine zones provided further insights into the mechanisms underlying diversity–environmental relationships. The models fit the data well for both Afromontane (Fisher’s \( C = 3.188 \), \( df = 2 \), \( p = 0.627; n = 60 \); Figure 3b) and the Afroalpine zone (Fisher’s \( C = 0.779 \), \( df = 2 \), \( p = 0.677; n = 55 \); Figure 3c). Together, the predictors explained 24% of the variation in plant species richness in the Afromontane and 82% in the Afroalpine zone. While fire frequency was the most important determining factor of plant richness variation throughout the entire elevation gradient, precipitation became much more important, especially in the Afromontane zone (direct effect = –0.902, \( p < 0.001 \)). Both in the Afromontane and Afroalpine zones, there was no longer an indirect temperature effect on plant species richness via fire frequency. Only in the Afroalpine zone, fire frequency retained a positive effect on plant cover. In contrast to the Afroalpine zone, precipitation had a direct positive effect on the richness of soil phototrophs in the Afromontane zone (direct effect = 0.454, \( p < 0.01 \)). Finally, in contrast to the Afromontane zone, there was a significant positive relationship between the bryophyte–lichen cover and plant richness in the Afroalpine zone.

4 | DISCUSSION

Our study illustrates a basic ecological principle regarding diversity patterns across communities that emerge locally from the complex and interconnected effects of abiotic factors (climatic and edaphic), disturbance and biotic factors (see also Grace et al., 2016; Lehmann & Parr, 2016). Consistent with previous studies, patterns and drivers of diversity changes varied between the three primary producer groups studied (Bruun et al., 2006; Bryant et al., 2008; Grau et al., 2007; Peters et al., 2016), presumably reflecting their difference in adaptations to abiotic and biotic conditions (i.e. stress tolerance and competitive ability). For instance, we found a hump-shaped variation in species richness along both gradients of elevation and standing biomass approximated by total plant cover. While this pattern is consistent with long-standing hypotheses (Grime, 1973; Huston, 1979) and with observations from many herbaceous (Fraser et al., 2015, but see Grace et al., 2016) and mountain systems (Rahbek, 1995), it was only observed for vascular plants and not for bryophytes–lichens or soil phototrophs. Moreover, along our elevation gradient on Mount Cameroon, we found strong links between co-occurring primary producer guilds as well as vascular plant functional groups, which support the idea that the environmental change impacts on specific groups of organisms and their biogeographical distribution should not be considered in isolation (Peters et al., 2016; Wisz et al., 2013).

Finally, by resolving the direct and indirect effects of macroclimate, edaphic conditions, disturbance (fire frequency) and various groups of primary producers generating the mid-elevation peak for vascular plants, our study revealed that the effects of energy and water on species richness pattern are largely mediated by disturbance, and their respective role is strongly dependent on the extent of the gradient considered (Field et al., 2009; Nogués-Bravo et al., 2008). 4.1 | Direct, indirect and scale-dependent effects of macroclimate and fire disturbance

When considering the full range of the elevation gradient, macroclimate variables appeared to be strong determinants of the diversity pattern, consistent with many previous studies (Hawkins et al., 2003; McCain & Grytnes, 2010; Peters et al., 2016). For instance, the shift in cover between C4 and C3 species along our elevation gradient is consistent with the temperature role described along other elevation gradients (e.g. Edwards & Still, 2008), or at global scale (Ehleringer et al., 1997; Still et al., 2003). Altogether, the specific response of the plant functional groups to climate likely contributes to the observed mid-elevation peak in vascular plant species richness on Mount Cameroon. The location of this peak, corresponding to the transition zone between the two principal vegetation types, the Afromontane and the Afroalpine zone, also aligns with previous observations conducted in a variety of mountain regions (Lomolino, 2001 and references therein). However, although deriving a direct causal relationship from these correlations is compelling and is commonly used to predict species distribution and explain diversity patterns, we show here that the impact of climate variables on plant species richness is largely mediated by other factors.

Expectedly, fire frequency proved to have a prominent role on plant cover or richness in our system, which includes savanna-like vegetation (Lehmann et al., 2014). In addition to climate, which is traditionally considered the main regulator of ecosystem characteristics and biogeochemical cycles, fire is an important factor in many ecosystems around the world and can shift or permanently change these systems (Pausas & Ribeiro, 2017). This is especially the case in savanna systems, where the interaction between trees, C4 species and fire is very well documented (Bond, 2008; Lehmann et al., 2014). It is interesting to note that in other areas of Cameroon, the natural tree line extends well beyond 2000 m (Cheek et al., 2000), and the presence of C4 savanna-like vegetation at lower elevations (and lower abundance of shrub) along our gradient is largely due to the occurrence of frequent fire (Keay, 1955; see also Bond, 2008; Cardoso et al., 2021; Lehmann & Parr, 2016). Because fire correlates with temperature and precipitation (see also Lehmann et al., 2014), it had
a strong mediating effect on species richness in Mount Cameroon. The omission of the role of disturbances like fire in our case, and probably other types of disturbance correlating with macroclimate variables in other systems (e.g. land-use, grazing, see Prach & Walker, 2020 for review; see also Nogués-Bravo et al., 2008), could lead to a possibly overlook of the association between intermediate disturbance and peak species richness (intermediate disturbance hypothesis, Connell, 1978; Grime, 1973). This would provide a largely incomplete description of the diversity pattern or even a false conclusion about the effects of the macroclimate (see also Chauvier et al., 2021).

By considering the Afromontane and Afroalpine zones separately, we demonstrated the importance of the extent of environmental gradients studied, the climatic domain examined, and the scale dependency of the drivers (Lehmann et al., 2014; Nogués-Bravo et al., 2008). On the one hand, some relationships hold irrespectively, such as the positive correlation between temperature and fire frequency observed in both parts of our elevation gradient, throughout its entire range, or even across African savannas in general (see Lehmann et al., 2014). On the other hand, the role of other drivers is more sensitive to the aforementioned geographical contingencies. For instance, the effect of temperature on species richness was observable only at the full extent of the elevation gradient, which encompassed a wider temperature range (from 17 to 3°C) and was mostly mediated by fire frequency. The influence of reducing the range of elevation on the strength of the relationship between climate variables and species richness is not entirely surprising in itself. Yet, it should be noted that each part still corresponds to a temperature range of c. 7°C. To put it into perspective, 7°C would correspond to at least 1000 km on a latitudinal gradient outside the tropics. It far exceeds global mean temperature projections and it is on pare with warming predictions from the highest emission scenarios in most vulnerable regions (i.e. polar regions). More generally, the role of our drivers and their interplay identified over the entire elevation gradient seemed to be primarily influenced by the Afromontane zone (82% variance explained), while their explanatory power was much lower in the Afroalpine zone (24% variance explained), where other unmeasured drivers were likely to explain the pattern (e.g. soil temperature, soil water potential, microtopography, etc.). Overall, this scale dependency is an important aspect of biogeographical studies, which has an immediate consequence on our inference about the role of different drivers of species richness patterns (Field et al., 2009; Nogués-Bravo et al., 2008).

4.2 | Bryophyte–lichen and soil phototroph diversity patterns, and inter-guild interactions

The mid-elevation peak in species richness observed for vascular plants did not apply to the two other guilds of primary producers (see also Bruun et al., 2006; Grau et al., 2007). Although both bryophytes–lichens and soil phototrophs showed an increase in abundance towards the harsher conditions found at high elevations, their diversity patterns also differed along the elevation gradient (monotonic increase vs. U-shaped variation). Our results therefore support the conclusion that ‘the forces structuring microorganism and macroorganism communities along elevational gradients differ’ (Bryant et al., 2008). This conclusion can be further extended because our findings suggest that the forces structuring different groups of microorganisms constituting the soil phototroph guild also differ.

Besides these idiosyncratic patterns of species richness, both bryophytes–lichens and soil phototrophs are also influenced by climate variables (Di Nuzzo et al., 2021; Rodríguez-Caballero et al., 2018), the former correlated primarily with temperature and the latter to precipitation. These observed correlations apply to the full range and the two parts of our elevation gradient and also align with previous experimental findings (e.g. Baldauf et al., 2021), suggesting that these different responses could be partially explained by contrasting physiological tolerance. However, as with vascular plants, the effect of climate variables on bryophytes–lichens and soil phototrophs was also mediated by other factors, with fire playing a central role (see Palmer et al., 2020 for review). The influence of climate also largely depended on whether we analysed the entire elevation gradient or two distinct zones separately. Here again, our results illustrate the complexity of elevation gradients and the difficulty of drawing strong conclusions about the mechanisms that produce biogeographical patterns from simple correlations.

The complex and indirect effects of macroclimate variables and fires producing our emergent pattern become even clearer when we consider the correlations between primary producer groups or plant functional groups. Although this does not necessarily imply that these species compete or facilitate each other (Barner et al., 2018; Liancourt & Dolezal, 2021), compelling evidence from other ecosystems suggests that in addition to capturing differences in physiological tolerance, some correlations may indeed reflect positive or negative interactions (i.e. facilitation or competition; Bruun et al., 2006; Freestone, 2006; Gavini et al., 2019; Rehakova et al., 2017). This is especially the case when the trade-off between competitive response ability and stress tolerance observed in vascular plants is at stake in other guilds as well (Liancourt et al., 2005). Competition and facilitation between (and within) guilds can therefore contribute to diversity patterns along our elevation gradients (Grime, 1973; Hacker & Gaines, 1997). For instance, the direct negative relationship between plant cover and bryophytes–lichens aligns with the competitive interactions often described between the two groups (e.g. Bruun et al., 2006). In contrast, the positive relationship between plant richness and the richness of phototrophs or C4 graminoids and Oscillatoriales may result from the positive effect of abundant cyanobacterial N-fixers on plant community development through soil nitrogen enrichment, water uptake and retention or increased soil stabilization (Rodríguez-Caballero et al., 2018), and consequently may facilitate the persistence of other organisms. Also, the positive correlation between plant richness and bryophyte–lichen cover in Afroalpine
zone may result from the bryophyte–lichen facilitative effect on plant germination, establishment or their performance in cold, humid and windy summit areas (see Figure S6) through likely soil stabilization, thermal amelioration, water and nutrient supply and protection against strong desiccant winds (Freestone, 2006; Gavini et al., 2019 and references therein).

4.3 | Effect of edaphic conditions on diversity patterns

Finally, edaphic conditions, here the soil N:P ratio, also accounted for some variations in plant species richness when we considered the full extent of the elevation gradient. This relationship can be better understood by examining the variation of N and P individually along our elevation gradient. Total soil N is strongly associated with soil organic matter and is therefore higher at low elevations, while the highest elevations have young and poorly developed soil with little organic matter and therefore low N content. Conversely, soil P is primarily derived from parent material (Vitousek et al., 2010 and references therein) and is expectedly higher in the Afroalpine zone with weathering of the young volcanic substrate. We could have expected a linear decline of soil P with decreasing elevation and the presence of more developed soils (Vitousek et al., 2010), but this was not the case. Instead, elevated P values in fire-prone Afrotropical grasslands are probably released by fire combustion and charring of vegetation, causing large losses of both C and N contained in plant biomass (and thus the soil organic matter) due to volatilization (Hogue & Inglett, 2012), while most P is thought to remain in plant residual ash and char (Veldhuis et al., 2016), and together with soil cations (K), become readily available for plant growth (DeBano et al., 1998). Consequently, our species-rich mid-elevation grasslands had the lowest phosphorus content but high concentrations of nitrogen (and hence the highest N:P ratio), which supports the conclusion from other grasslands (Palpurina et al., 2019) where high phosphorus availability usually leads to the dominance of only few species and low overall diversity (Doležal et al., 2019). Altogether, because it correlated with precipitation along our elevation gradient, the effect of soil N:P ratio on species richness, if not considered explicitly, could be easily attributed to climate.

5 | CONCLUSIONS

We showed that although our pattern of species richness could be attributed and explained by the energy/water hypothesis, this pattern emerges from the complex direct and indirect effect of multiple factors. Our results fully agree with the statement of Lomolino (2001) about how general patterns in nature emerge from the combined effects of many redundant or convergent processes. In our case, intermediate disturbance, intermediate biomass, intermediate stress, contact between zone (ecotone), edaphic/nutrient, together with energy/water all contribute to the mid-elevation peak in species richness. This finding and identification of mediating factors, such as fire disturbance, together with the fact that climate effect is largely dependent on the scale and extent of the studied gradients illustrate the challenges of predicting the future of species richness without taking into account the complexity of diversity patterns.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at https://doi.org/10.5061/dryad.gf1vhhmqv (Doležal et al., 2022).

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BIOSKETCH
The Institute of Botany of The Czech Academy of Sciences has been conducting botanical research on Mount Cameroon since 2011. The main focus has been aimed at explaining vegetation patterns in relation to environmental gradients, long-term vegetation monitoring, the role of climate, disturbances and inter-guild interactions behind the elevational patterns of vascular plants.

AUTHORS’ CONTRIBUTIONS: J.D., M.D. and P.L. conceived the ideas and designed the methodology; J.D., M.D., J.A., L.M., J.K. and J.V. collected the data; J.D. and P.F. analysed the data; and J.D. and P.L. led the writing.

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