Latitudinal Patterns of Bryophyte Diversity in Africa

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Abstract: TESHOME SOROMESSA (2026): Latitudinal Patterns of Bryophyte Diversity in Africa. *Frahmia* 54:1-21*.

The latitudinal diversity gradient is one of the most persistent patterns in biogeography, but its expression varies among taxonomic groups and environments. Bryophytes provide a useful test of this pattern because mosses, liverworts and hornworts are poikilohydric, depend strongly on atmospheric moisture, and occupy fine-scale substrates that are often overlooked in continental biodiversity assessments. This article synthesizes evidence on bryophyte richness, composition, endemism and turnover across African countries and major island systems. The synthesis covers the Mediterranean Maghreb, Saharan and Sahelian belts, Guineo-Congolian forests, Afromontane systems, the Albertine Rift, Eastern Arc Mountains, Madagascar and the Western Indian Ocean islands, the Zambezian region, and the Cape and Succulent Karoo systems. The evidence does not support a single, continent-wide curve in which richness rises steadily toward the equator and then declines symmetrically. Instead, the African pattern is better described as a set of regional richness centres shaped by water availability, elevation, cloud immersion, habitat heterogeneity, substrate conditions, climatic history and sampling intensity. Humid tropical mountains are particularly important because they combine thermal relief with persistent atmospheric moisture and a large number of microhabitats. Tropical lowland forests remain important for leafy liverworts and epiphytes, while Mediterranean and winter-rainfall regions support distinctive drought-tolerant bryofloras. The interpretation is constrained by uneven collecting effort and differences in taxonomic coverage. O'Shea's checklist records 2,939 moss taxa for sub-Saharan Africa and adjacent islands, while Wigginton's fourth edition lists 1,118 accepted liverwort and hornwort taxa for sub-Saharan Africa and the East African islands. These inventories demonstrate the scale of the flora but do not by themselves provide standardized richness estimates by latitude. Consequently, claims of a continental maximum should be treated as synthesis-level interpretations rather than as the output of a single comparable sampling design. The article identifies major evidence gaps and proposes standardized elevational transects, coordinated herbarium digitization, molecular revision of difficult groups, and repeated microclimate measurements.

Keywords: Bryophyta; Marchantiophyta; Anthocerotophyta; latitudinal diversity gradient; Afromontane forests; elevational diversity; endemism; Africa; bryogeography; species richness.

1. Introduction

Spatial structuring of biological diversity has been a topic of great interest in ecology and biogeography. Species richness often increases towards lower latitudes, peaking in tropical regions and decreasing towards temperate and polar areas (Gaston, 2000; Hillebrand, 2004; Willig et al., 2003). Multiple theoretical frameworks have been proposed, ranging from energy availability and climate to evolutionary time, area, and speciation–extinction dynamics, but no single mechanism appears to account for all patterns (Mittelbach et al., 2007). Bryophytes offer an interesting perspective on this debate.

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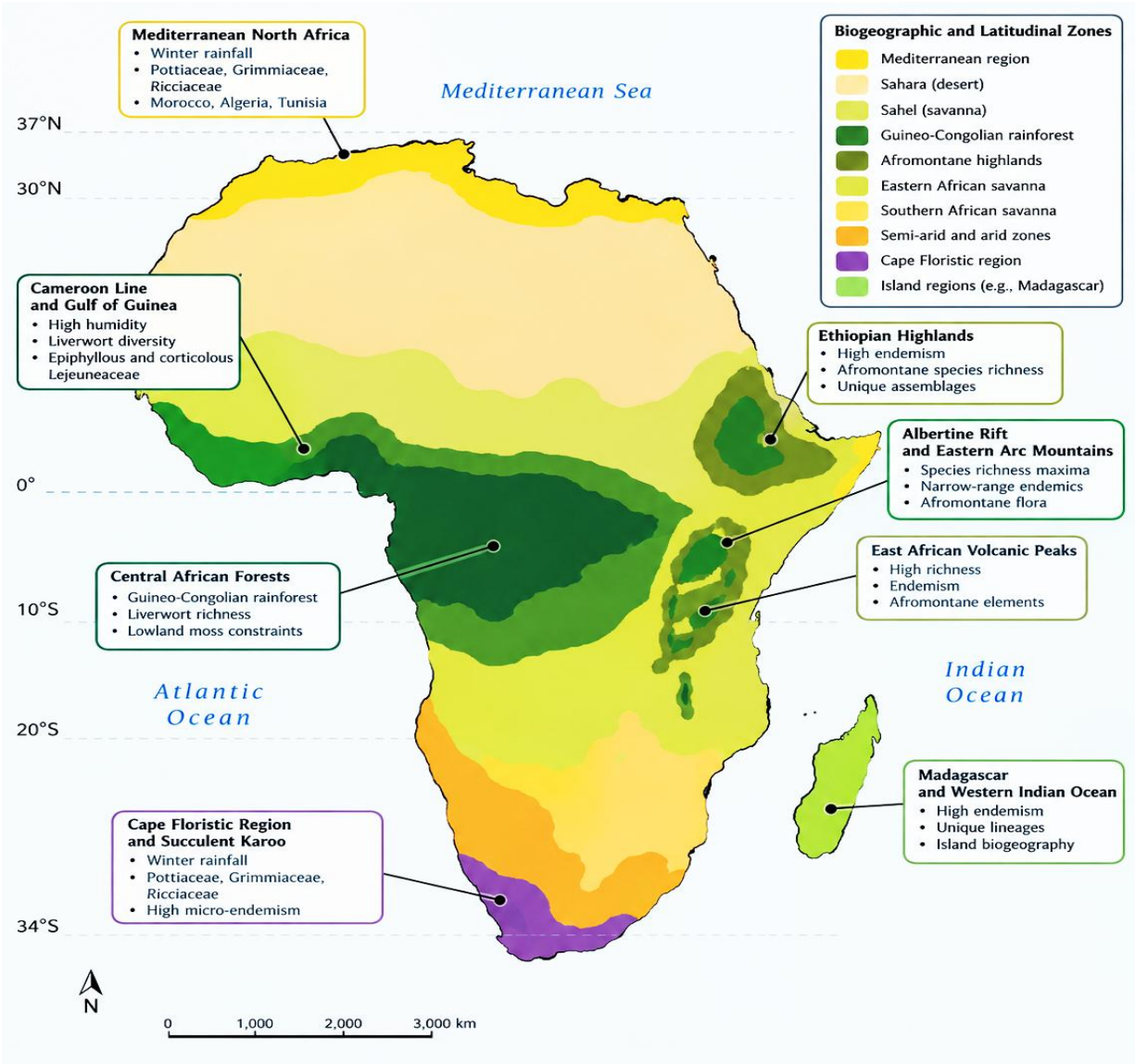

Figure 1: Schematic illustration of the primary biogeographical regions used in this synthesis. Note that this figure is merely an approximate guide; no formalised geographical analysis was performed.

As non-vascular plants, mosses, liverworts, and hornworts typically rely on external water sources for their internal hydration, and gas exchange and photosynthesis are often severely limited during desiccation (Proctor et al., 2007; Oliver et al., 2005). Consequently, bryophyte richness is partially determined by the frequency, duration, and patterns of precipitation, cloud cover, canopy openness, and the water-holding capacity of the substrates (Proctor et al., 2007; Oliver et al., 2005). At the same time, the ability of some bryophytes to resist desiccation can allow them to occupy niches with otherwise insufficient moisture. Africa is a continent with a large latitudinal span, encompassing Mediterranean, temperate, and winter-rainfall climates in the south, the Sahara Desert, the Sahel, the Guineo-Congolian rainforest, savannas, Afromontane forests, volcanic regions, ancient crystalline formations, coastal habitats, and large islands. Moreover, Africa hosts numerous endemic lineages of bryophytes, providing further potential for richness structuring beyond mere latitude.

The data show that the richness patterns of bryophytes recorded in Africa do not display a simple peak at the equator but have several centres in the tropical mountain areas as well as in northern and southern Africa. This observation is true for mosses but is even more prominent for liverworts and hornworts. The same applies to other continents, but the pattern is not universal across all bryophyte taxa and remains poorly understood (Geffert et al., 2013; Shaw et al., 2005). Another

crucial observation is that richness is partially determined by the number of botanists who have studied a given region. O'Shea (2006) argued that continental checklists of bryophytes are a necessary precondition for conservation and ecological research, while Wigginton (2018) created a country-level distribution list for liverworts and hornworts. Thus, a checklist with a large number of entries is indicative of both high scientific interest and biological richness, but a low number of entries might be a sign of neither. Therefore, the purpose of this article is not to impose an artificial curve on the findings but to highlight the interactions between latitude and other factors that determine the distribution of bryophyte richness in Africa. Particular attention will be paid to analysing the trends in regional studies with varying foci.

Review objectives

This synthesis will address four questions. First, what is the distribution of bryophyte richness and taxonomic diversity in Africa at various latitudes? Second, how do elevation changes modify this pattern, especially in mountainous areas near the equator? Third, what are the key abiotic and biogeographical factors that structure bryophyte diversity? Fourth, where are the most critical evidence gaps located?

Working interpretation of the latitudinal gradient

In this article, the term latitudinal gradient refers to any spatial pattern, be it monotonic or multimodal, that connects species richness with latitude. Figure 1 below provides a rough visualisation of the African latitudinal zones relevant to this study. A gradient in this article refers to either a steady increase or decrease in richness, while a multimodal pattern has more than one peak.

2. Conceptual and taxonomical background

Bryophytes in this review include mosses, liverworts, and hornworts. Modern phylogenetic studies tend to split these organisms into Bryophyta, Marchantiophyta, and Anthocerotophyta, but the systematics of each group remains debated (Söderström et al., 2016) (see Table 1). Following regional continental studies, this review retains the old classification for simplicity, as many African checklists still utilise it.

Group	Principal African habitats in the reviewed evidence	Common ecological signal	Main evidence limitation
Mosses (Bryophyta)	Montane forests, rock, soil, tree trunks, logs, Mediterranean habitats, arid soil crusts	Strong response to moisture, substrate and elevation; conspicuous drought-tolerant forms in seasonal climates	Many inventories are incomplete at microhabitat level
Liverworts (Marchantiophyta)	Humid forest, tree bark, leaves, logs, cloud forest, seasonal soil	High representation of leafy liverworts in humid forests; thalloid forms important in seasonal environments	Taxonomic identification is demanding; canopy sampling is uneven
Hornworts (Anthocerotophyta)	Moist soil, disturbed ground, riparian and agricultural margins	Often local and seasonal; ecological patterns less completely documented	Small literature base and limited country-level sampling

Table 1: Taxonomic groups

Ecological role and gradients

The gradient in bryophyte diversity is partially explained by the organisms' unique physiology. Precipitation alone is not the sole driver of richness, as frequent but short-term deluges may be insufficient to support bryophyte growth. Rather, the key determinant is the frequency and duration of water availability, including nocturnal humidity in shaded areas. For example, desert microhabitats with seasonally available water can sustain bryophyte life, while a humid valley with a closed canopy may fail to do so due to high temperatures and competition with vascular plants. Meanwhile, the ability of some bryophyte species to withstand desiccation is yet another factor that increases their diversity in seasonally arid environments. The supplied manuscript provides a detailed discussion of the anatomical and physiological adaptations that allow bryophytes to survive dry spells, including cellular repair mechanisms during rehydration (Proctor et al., 2007;

Oliver et al., 2005). Therefore, bryophyte diversity in the Mediterranean and southern Africa is not lower than in the adjacent humid tropics but is shaped by different conditions.

3. Methods

The checklist, taxonomic, regional, and ecological evidence cited in it were used in this study. Additional evidence was collected to evaluate the claims made in the draft, primarily O'Shea (2006), Wigginton (2018), the PRISMA 2020 guideline for systematic reviews, and the scholarly articles on moss diversity mentioned in the draft. The latter resource describes the PRISMA 2020 recommendations in detail (Page et al., 2021). Notably, PRISMA 2020 promotes reporting the protocol and methods of a systematic review while following a set of recommendations, including a precise description of the search and screening process. However, this article does not report a systematic review but a synthesis of the evidence. The reason is that the supplied draft does not contain the search results in their entirety. Specifically, there are no verifiable numbers for the record inclusion and screening stages. Therefore, for the purposes of this review, the synthesis of the evidence found was conducted, rather than a systematic review with statistical analysis. This nuance may be revised if a full set of search results is provided later.

Search strategy

The search was initially conducted across scholarly databases, including Web of Science, Scopus, Google Scholar, African Journals Online, the Biodiversity Heritage Library, and relevant bryology journals. The search strategy aimed to identify articles and books that addressed bryophyte diversity in Africa. The key concepts included taxonomic terms, African geographical names, and diversity-related keywords. Additionally, older literature that did not use modern electronic databases was reviewed.

Inclusion criteria

Criterion	Included	Excluded
Organisms	Mosses, liverworts and hornworts with identifiable geographic information	Vascular plants, lichens, fungi and algae without separate bryophyte data
Geography	African mainland countries and relevant African islands	Regions outside the African biogeographic scope
Evidence type	Checklists, floras, field inventories, transects, taxonomic revisions and ecological studies	Anecdotal records without verifiable provenance and unsupported opinion
Data quality	Documented taxa, locality or coordinates, and habitat context	Unverifiable identifications, duplicate records and records without geographic context
Languages	English, French, German, Spanish and Portuguese where relevant evidence was accessible	Material lacking sufficient bibliographic or taxonomic information

Table 2: Inclusion criteria used in this review

Data extraction

Field	Information recorded	Interpretive value
Geographic position	Country, locality, latitude, longitude	Places records on the continental gradient
Elevation	Minimum and maximum elevation, or elevation bands	Separates latitude from thermal and cloud effects
Taxonomic scope	Mosses, liverworts, hornworts, families and genera	Identifies taxon-specific responses
Habitat	Forest, cloud forest, savanna, desert, rock, soil, epiphyte, riparian habitat	Links richness to habitat structure
Richness	Reported species counts, alpha diversity or checklist totals	Provides local or regional evidence of diversity
Turnover	Changes among sites, elevations or habitat types	Assesses beta diversity and replacement
Environment	Rainfall, humidity, temperature, canopy, substrate	Identifies recurring ecological drivers
Evidence quality	Voucher information, sampling design and geographic precision	Separates biological signal from sampling artefact

Table 3: The procedure of data extraction

Quality assessment

Three types of biases are particularly relevant to this review. First, spatial bias occurs when diversity assessments focus on readily accessible locations, such as mountainous zones, road edges, research stations, and national parks. Second, taxonomical bias arises from uneven efforts to document mosses, liverworts, and hornworts, which can mask true diversity patterns. Third, methodological bias complicates the comparison of richness between studies that use different sampling strategies, such as floristic surveys versus plot-based ones. Accordingly, this synthesis uses richness as an indicator of diversity within a study rather than comparing these values between studies. The differences between regions were evaluated in the context of spatial, taxonomical, and methodological biases.

4. Results

Continental evidence base

Two major checklist literature sources provide a reasonable assessment of the size of the African bryoflora. O Shea's checklist (fifth edition) contains 2,939 moss taxa for sub-Saharan Africa and the regions' islands. Wigginton's fourth edition lists 1,118 accepted liverwort and hornwort taxa for sub-Saharan Africa and East African islands. The figures are not additive due to differences in taxonomic, synonymy, biogeographical, and nomenclatural approaches used in the two checklists. Nevertheless, the numbers are a sign of the bryoflora's vastness that requires dedicated taxonomic infrastructure for its proper understanding.

The review literature is not distributed evenly across the continent. East African mountains, the Cameroon Line, Madagascar, the Cape region, and Mediterranean countries have been the focal points of taxonomic research. The Congo Basin, Sahel and Sahara, Angola, Mozambique, and the Horn of Africa are underrepresented in the reviewed bibliography. This is an important consideration because the evidence is skewed toward individual biogeographical regions, which may have influenced the interpretation of the continental patterns.

Latitudinal zones and documented diversity

Latitudinal sector	Representative regions	Documented pattern	Principal controls	Confidence
30°N to 37°N	Morocco, Algeria, Tunisia	Rich Mediterranean bryoflora with drought-tolerant mosses and seasonal liverworts	Winter rainfall, Atlas relief, seasonal drought, substrate diversity	Moderate to high for well-studied localities
15°N to 30°N	Sahara and Sahel	Low recorded richness with localized refugia	Severe water limitation, high evaporative demand, ephemeral moisture	Low to moderate because sampling is sparse
10°N to 10°S	Cameroon, Uganda, Rwanda, DRC, Kenya, Tanzania, Ethiopia	High diversity in humid forests and especially montane systems	Cloud immersion, elevation, habitat heterogeneity, moisture	Moderate; strong regional studies but uneven continental coverage
10°S to 28°S	Madagascar, Zambezian and miombo regions	Strong regional contrasts between humid mountains and dry woodland	Island isolation, rainfall gradients, elevation, dry-season stress	Moderate for Madagascar; lower for several mainland areas
28°S to 34°S	South Africa, Cape Floristic Region, Succulent Karoo	Distinctive southern assemblages including drought-tolerant terrestrial bryophytes	Winter rainfall, topography, soil crusts, seasonal drought	Moderate to high in intensively studied regions

Table 4: Latitude zones, representatives and their patterns

The pattern depicted in Figure 2 is intentionally schematic. The most prominent signal in the reviewed literature is the association of species richness with tropical mountains. The second richness peak is found in the Mediterranean, North Africa, and the Saharan winter rainfall zone. The latitudinal gradient in Figure 2 is partially explained by the documented decrease in moisture availability beyond the tropics. Nonetheless, the absence of steep declines in central Africa and eastern Madagascar suggests that these regions may have higher species richness than the gradient implies.

Tropical lowlands

The Guineo-Congolian forest region supports a significant bryoflora diversity, especially in terms of leafy liverworts and their various epiphytic, epiphyllous, and corticolous associations. The checklist literature provides a rough baseline of moss and liverwort diversity across sub-Saharan Africa. Yet, the review literature suggests that regional variations may be substantial, especially due to differences in forest types and local relief. Lowland rainforests are not biodiversity “deserts” of bryophytes, but their alpha diversity may be challenging to estimate because of the uneven distribution of species among substrates. A particular consideration for lowland forests is the diversity found on epiphytic and corticolous substrates. Species found on these substrates can occupy a range of microhabitats at various levels of the canopy. Therefore, a survey of the forest floor will miss many taxa that occur on the leaves and the bark. The same relative diversity shortfalls may be observed when comparing closed-canopy forests to the more open landscapes typical of Mediterranean climates. These comparisons are only approximate, however, given the complexities of bryophyte ecology.

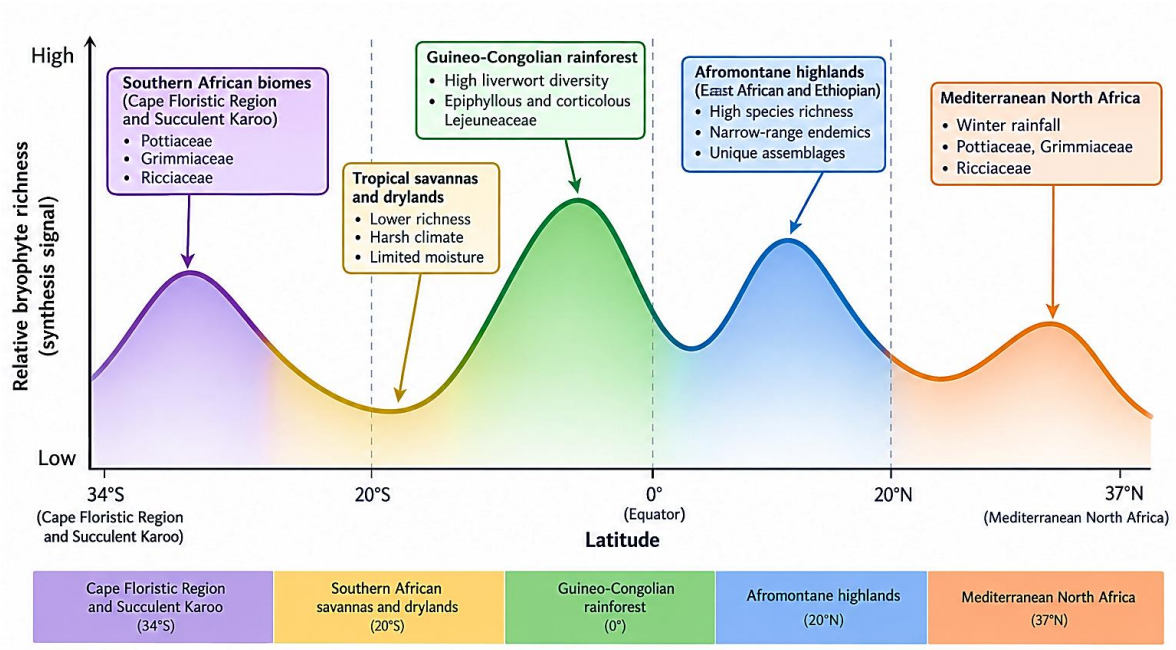

Figure 2: Conceptual latitudinal profile of documented bryoflora richness. The y-axis is an approximate synthesizing value, not a formal species richness metric. The curve reflects the pattern derived from the reviewed literature and should not be interpreted as a mathematical model.

Afromontane systems

The pattern of regional richness across latitudes is best approximated by the distribution of species in tropical mountains. Tropical and subtropical montane regions appear to be the most diverse in terms of bryophytes. This is not exclusively a matter of vertical diversity, however, since the mountains often intersect other gradients. They host multiple isolated habitats with varying moisture regimes, substrates, and exposure. Moreover, the mountains create a mosaic of regional biomes, each of which harbors a distinct set of bryophyte taxa. The study by Frahm (1990) on Mount Cameroon is representative of the whole region. It demonstrates how bryophyte diversity varies with elevation through diverse associations of liverworts, mosses, and hornworts. Similar trends can be observed in the broader survey by Frahm and Gradstein (1991). It connects bryophyte ecology with variations in forest zonation typical of tropical mountains. The same principles apply to the Afromontane region with the caveat that each locality has its own elevational diversity peak.

Endemism and beta diversity

Endemism is a common challenge for plant geography on a continental scale. Bryophyte species typically have large distribution ranges due to the ease of spore dispersal. Narrow endemics can arise in isolated habitats with favorable conditions, which can contribute to beta diversity. The mountains of the Eastern Arc, Albertine Rift, and Madagascar, in particular, are expected to have a significant number of range-restricted species. These localities should be prioritized in further research on continental bryoflora. Beta diversity presents another consideration, as similar latitudinal zones can host drastically different bryofloras. Different mountainous regions often have little overlap in their species lists. Even within a single mountain, alpha diversity can decrease drastically with elevation. A forest at 1,800 meters will have few bryophyte species in common with a dry woodland at 300 meters. By comparison, two lowland rainforests with comparable humidity and substrates can share a large number of species. This poses additional challenges for diversity assessment, as the beta diversity in lowland forests seems to be lower than in the highlands.

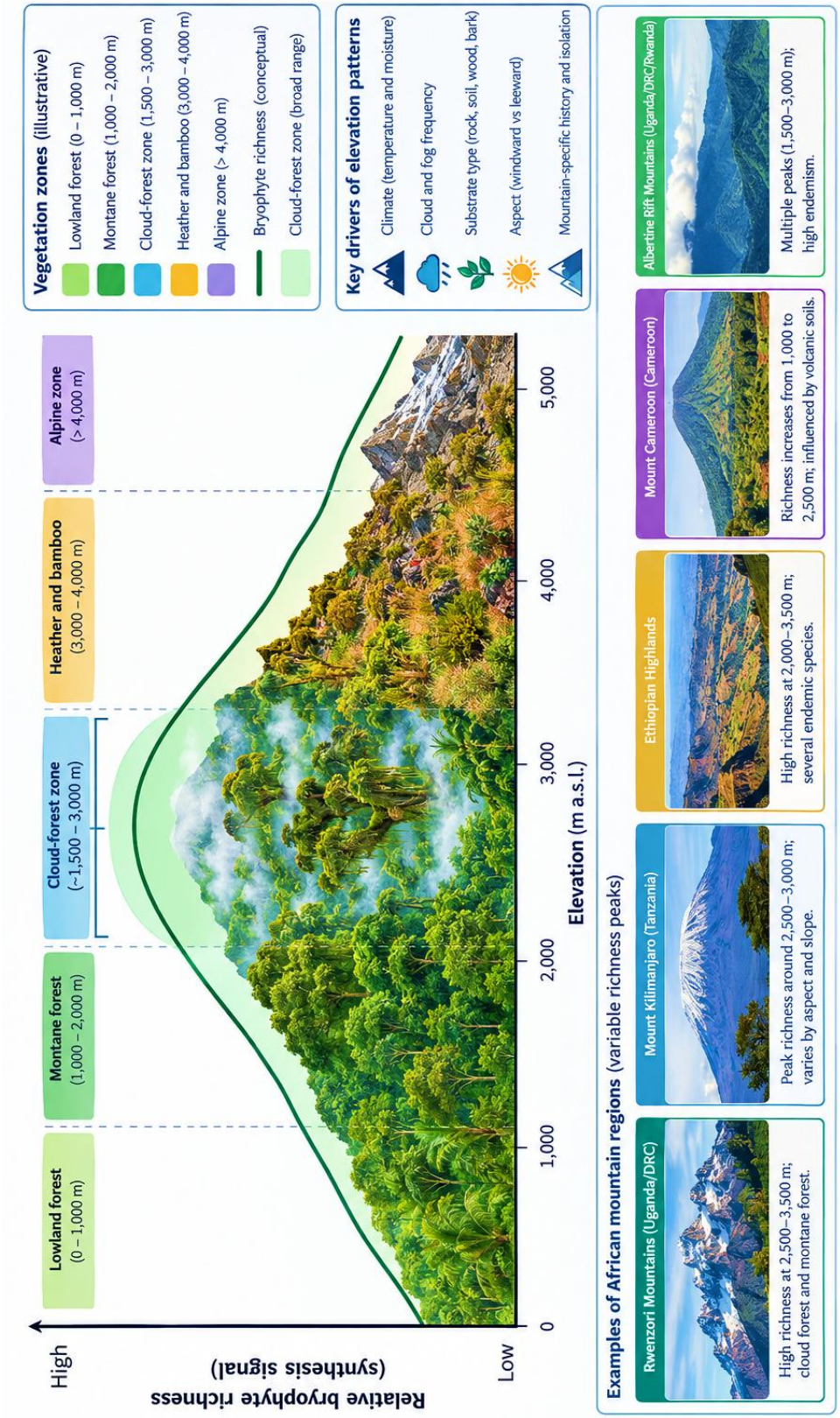

Figure 3: Conceptual elevational richness profile for African mountains. The cloud-forest interval is shown as a broad peak to reflect variability between localities. Note that the richness optimum varies between mountain ranges and is influenced by multiple factors beyond latitude.

Representative regional evidence

Region	Study or source	Principal evidence	What it contributes to the gradient question
Sub-Saharan Africa	O'Shea (2006)	2,939 moss taxa recorded in the checklist scope	Provides a taxonomic and country-distribution baseline for mosses
Sub-Saharan Africa and East African islands	Wigginton (2018)	1,118 accepted liverwort and hornwort taxa with country records	Provides a comparable distribution framework for hepatics and hornworts
Mount Cameroon	Frahm (1990); Frahm & Gradstein (1991)	Clear altitudinal zonation of bryophyte communities	Shows why elevation can modify a latitude-only interpretation
Bwindi, Uganda	Tusiime et al. (2007)	114 species recorded across three forest types	Demonstrates habitat and forest-type effects at local scale
La Réunion	Ah-Peng et al. (2007)	Elevational distribution studied on an oceanic island	Illustrates island elevation as a strong driver of turnover
Madagascar	Marline et al. (2019, 2020)	National checklist and Marojejy elevational study	Shows island isolation, elevation and climatic asymmetry
Mediterranean region	Ros et al. (2007, 2013)	Annotated checklists for liverworts, hornworts and mosses	Documents a northern extratropical bryoflora
Succulent Karoo	Hedderson & Zander (2007, 2008)	Diversity, endemism and new Didymodon species	Shows taxonomic differentiation in seasonal arid habitats

Table 5: Regional evidences

Regional case study I: Cameroon Line and Gulf of Guinea

The Cameroon Line is a good example of a latitudinal diversity center that is also shaped by topographical factors. The region encompasses lowland rainforests, submontane and montane forests, and high-altitude volcanic deposits. These variations lead to differences in bryoflora diversity, with the highest levels found near Mount Cameroon. The mountain's proximity to the equator may amplify the effect, increasing species richness beyond what is typical for the latitude. Frahm (1990) documented this pattern for bryophytes, describing how different altitudinal zones relate to changes in regional diversity. The mountain's role is important due to its influence on regional diversity in a continental context. The lowlands of the Cameroon Line are typical of lowland forests in general, while the upper reaches can reach the levels of cloud forests.

The review provides a practical message for field surveys that intend to characterize regional richness. Lowland forests will have a lower number of species compared to higher-altitude forests. However, some of the species found in the lowlands are absent in the highlands, suggesting that a comprehensive survey requires multiple elevation bands. Another observation specific to lowland rainforests is the diversity on epiphytic and corticolous substrates.

Regional case study II: Albertine Rift and Eastern Arc Mountains

The Eastern Arc Mountains and Albertine Rift are another region with high levels of diversity. They represent the second major diversity center for African bryoflora, with species richness comparable to that of the Cameroon Line. Eastern Arc Mountains are isolated mesic habitats surrounded by lower-altitude plains and forests. Albertine Rift is similar in some ways to the Eastern Arc but encompasses a greater variety of landforms, including volcanic and non-volcanic geological structures. The two regions are similar in terms of bryological evidence, with a strong focus on epiphytic liverworts and hornworts. Pócs (1976) was one of the first researchers to note the value of such vegetation in the Uluguru Mountains. Epiphytic bryophytes serve as an essential component of the forest ecosystem, participating in water storage and providing

habitat for other organisms. In turn, the Eastern Arc Mountains and Albertine Rift appear to boast one of the richest bryofloras in continental Africa.

Bwindi Impenetrable Forest is a good example of local beta diversity in Africa. The region hosts 114 bryophyte species in its lowland, submontane, and montane forests. According to Tusiime et al. (2007), these are the results of variation in forest types within a single region. Local beta diversity seems to be the major contributor to the overall species richness in the region. The practical implication of this finding is that a larger number of forest types must be surveyed to find the majority of local bryophyte species.

Regional case study III: Madagascar and the Western Indian Ocean

Madagascar is one of the few isolated landmasses in continental Africa. Its insular status has shaped the island's biogeography, which in turn has diversified its bryoflora. Marline et al. (2019) provide a comprehensive overview of the country's bryology in general, while Marline et al. (2020) analyze the patterns of elevational diversity. Together, the studies demonstrate that Madagascar's bryoflora is distributed across a wide range of environments. From a continental perspective, the island's isolation is what distinguishes it from other regions.

The island's eastern coast and hinterland intercept the moisture-laden winds from the Indian Ocean, resulting in high rainfall. Meanwhile, the central and western areas of Madagascar experience the effects of the rain shadow and are considerably drier. These variations create a wide diversity of microhabitats within a single territory, which explains the findings on beta diversity. Local bryofloristic surveys can see drastic changes in species lists at different elevations due to variations in rainfall, temperature, and associated substrate.

Another finding of the survey literature is the potential endemism in Madagascar's bryoflora. This is a continuation of the patterns observed in the Eastern Arc Mountains, with Marline et al. (2020) noting several narrow endemics within the Marojejy National Park. The number of endemic species in Madagascar may be even higher due to the island's isolation and its unique bryological heritage. However, endemicity can prove difficult to assess for historical reasons. Reeb and Bardat (2014) review discusses the nomenclatural challenges in the bryoflora of Madagascar. Some of the species identified as endemic may have been overlooked due to synonymies.

Regional case study IV: Mediterranean North Africa

The Maghreb region of North Africa is the northernmost part of the continent, with a Mediterranean climate that sustains a distinct biome. The region has a considerable range of habitats, from the Atlantic coast and coastal plains to the Atlas and Rif mountains. The mountains support a rich bryoflora, which is further enhanced by the presence of seasonal streams and seepages. Ros et al. (2007) and Ros et al. (2013) provide annotated lists of liverworts, hornworts, and mosses of the region. Taken together, the studies show the diversity of bryophytes in North Africa and their relationship to the local environment.

Pottiaceae and Grimmiaceae are both widespread but have adapted to the local seasonality. Species of these two families can survive the dry summers by staying dormant and re-emerging with the onset of the rains. Thalloid liverworts, when present, also favor the wet-rainfall season. Due to both their abundance and adaptability, bryophytes of North Africa can maintain a relatively high diversity in a region with a limited growing season.

The Maghreb region also serves as a useful reference for discussions of regional bryofloristic diversity. The review literature on North Africa rarely uses the term "richness peak," with the emphasis instead placed on diversity patterns across different substrates and vegetation types. Any discussion of bryofloristic diversity in the Maghreb should acknowledge the limitations of the published lists. A checklist of the region's bryoflora covers the entire territory, which reduces the diversity value of any individual entry. The phrase "regional diversity centre" is more appropriate to the findings of the review literature.

Regional case study V: Cape Floristic Region and Succulent Karoo

The Cape region and Succulent Karoo biome of South Africa provide another example of bryofloristic diversity in an extratropical region. Similar to the Maghreb, the Cape Floristic Region has a Mediterranean climate that sustains diverse bryophyte communities. The Succulent Karoo biome, in turn, is seasonal and semi-arid, but it hosts a number of bryophyte species nonetheless. Hedderson and Zander (2007) examine the patterns of bryofloristic diversity in the Succulent Karoo, and Hedderson and Zander (2008) describe some of the Didymodon species of the region. The findings demonstrate how varied the conditions can be within South Africa's biomes and the bryofloristic diversity they sustain.

Bryophyte species typical of the two regions include drought-resistant mosses and liverworts that grow on a variety of substrates. Some of the local species are found in other parts of Africa, but the biome also has several endemics. Due to

its seasonal nature, the Succulent Karoo supports a certain number of specialized species that are not found elsewhere on the continent. The same is true for the Cape Floristic Region, which has a number of bryophytes that are endemic to South Africa. However, the bryofloristic diversity of the Cape region and Succulent Karoo cannot be extrapolated to the entire subcontinent. South Africa's geology and climate are markedly different from the remainder of continental Africa. Even within the subcontinent, the similarities between the two regions are only partial.

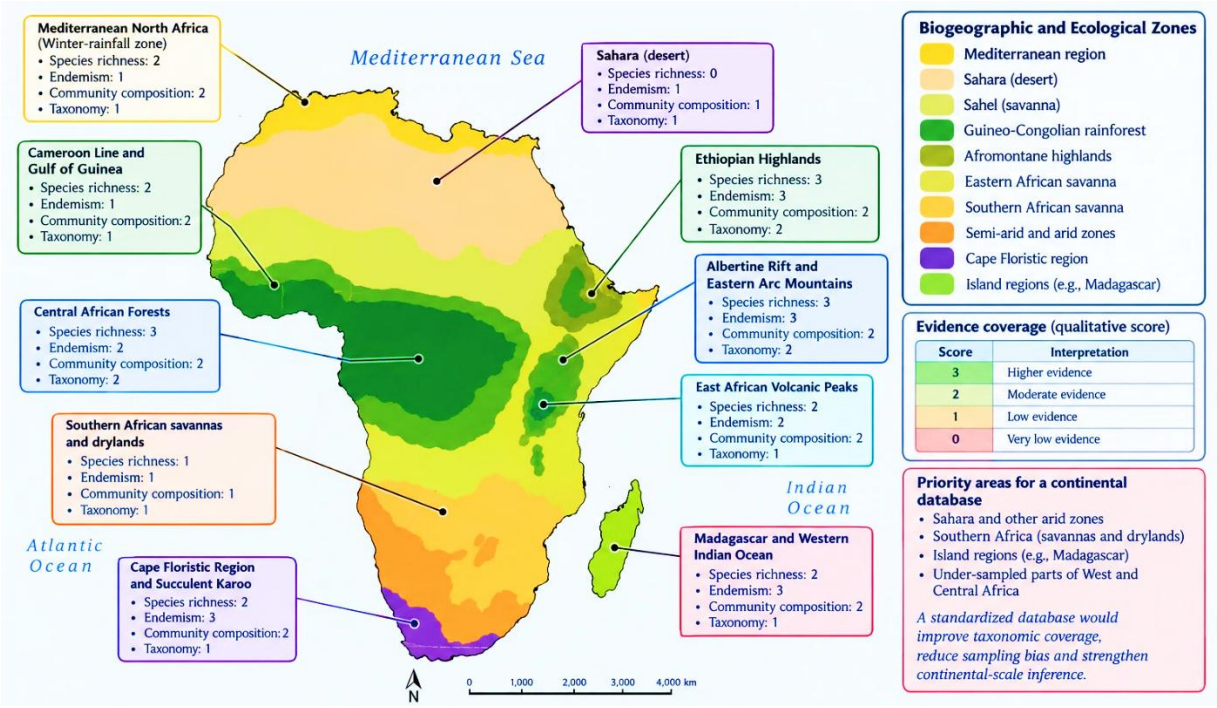

Figure 4: Relative evidence coverage inferred from the reviewed literature. Scores are qualitative synthesis categories, not measured database counts: 0 = very low, 1 = low, 2 = moderate, 3 = high. The figure highlights where a future standardized continental database would most improve inference.

5. Discussion

The African pattern is not adequately described by latitude alone

The main finding of this synthesis is that, while latitude is an organizing variable, it does not fully describe African bryophyte diversity. The most convincing evidence comes from individual places where large gradients in elevation and moisture have occurred within relatively narrow latitudinal spans. Within Mount Cameroon and the Albertine Rift, Eastern Arc, and Madagascar, significant variation in bryophyte richness accompanies topographical and aridity variation. These observations fit into the overall pattern of moss diversity having an ecological structure in addition to the broad latitudinal gradient (Geffert et al., 2013; Shaw et al., 2005). They also agree with findings that the latitudinal diversity gradient is not a universal property of biota but varies with region, taxa, and spatial scale (Hillebrand, 2004; Willig et al., 2003). Latitude is not unimportant, however. It organizes overall distribution patterns by controlling solar input and seasonal variation, large-scale circulation, and vegetation zonation. Latitude acts more like an encompassing geographical variable, one whose importance is expressed through multiple ecological factors.

Moisture is a central ecological axis

Moisture emerges as a critical component in almost all the considerations of this study. While bryophytes can survive in desiccated conditions, their growth and reproduction require periodic inundation or high humidity. Cloud forests are an excellent example of a habitat that satisfies this need through both rainfall and the additional moisture provided by cloud condensation. Another implication of the importance of water is that the contribution of montane habitats to diversity may not always be captured by rainfall data, since the additional input of water vapour and the lower temperatures at higher elevations also contribute to richer bryophyte communities. Moisture is a term that can cut across various levels of ecological relevance. Annual rainfall data for a given location may be useful, but it is arguably more informative to consider relative humidity, vapour pressure deficits, leaf wetness, and cloud immersion. Likewise, the degree of canopy

openness and the nature of the ground cover will affect how much moisture is retained or lost at any given time. Future studies should consider evaluating these variables.

Elevation modulates the thermal regime

Elevation is an especially important variable that strongly affects tropical climates. It can cause marked decreases in temperature that allow cooler montane habitats to host a wide range of life forms not found in lowlands. For bryophytes, the combination of lower temperatures with higher humidity allows these plants to thrive. As a result, many African mosses have a diversity gradient that follows elevation in addition to the latitudinal one. The pattern is not necessarily one of a richer community at every summit, however, since some of the most extreme examples of diverse mosses can be found in cloud forests. Above the tree line, wind, freezing temperatures, desiccation, and unstable growing conditions may lower overall diversity while favoured taxa take over. The pattern of richness in relation to elevation therefore often takes the form of a hump or several distinct zones.

Habitat heterogeneity and the diversity of substrates

Bryophytes utilise an unusually wide range of small-scale habitats. Most of their diversity can be seen on bark, leaves, and decaying woody matter, but a rich community often accompanies rock faces, wetlands, and exposed soil. On a larger scale, a forest with a great range of tree species and varied woody material will offer more potential homes for bryophytes than one with uniform vegetation. This observation leads directly to the conclusion that variation in habitat types and substrates is positively correlated with richness. It also suggests that conservation planning should account not only for forest types but also the importance of individual habitat "islands". A wet ravine within an otherwise dry region might well be significantly more diverse than the surrounding vegetation.

Sampling bias and the challenges of false gradients

It is essential for this kind of study to consider the issue of sampling bias. In other words, richness estimates must be corrected for the likelihood that a given area has been thoroughly surveyed. Some localities, such as popular mountains, may have an inflated number of specimens due to frequent visits by botanists. Meanwhile, a remote basin may have few known taxa even with considerable diversity. The difference between recorded and actual richness is especially pertinent for Africa, since many localities have been visited only once or twice.

Another issue is the possible bias in taxon discovery. Mosses have long been a taxonomically intensively studied group that has produced numerous publications. One might expect to find fewer species of liverworts and hornworts due to their relative lack of research. Likewise, canopy specialists are less likely to be found in plots studied by methods that only sample ground vegetation. The differences between localities may be due to these biases in discovery rather than true variation in richness. As a possible solution, future attempts at continental-scale analyses should incorporate information on sampling intensity. Plots with more visits, more days spent surveying, and more specimens collected should have lower estimated diversity. Likewise, richness estimates should take into account the number of herbarium specimens and the proportion of the target area covered by a survey. Methods such as rarefaction and extrapolation can be applied to standardize the comparison between localities.

Historical biogeography

The distribution of bryophytes also reflects historical patterns. In particular, the current richness distribution is largely a product of past changes in climate variability. Periods of intense aridity would have reduced the extent of forested and other humid habitats, fragmenting potential continuous distributions. The most likely locations for in situ survival would have been islands, coastal mountains, and isolated ranges that persisted through drier periods. These areas may well have been important diversity centres for many African bryophyte species.

The Eastern Arc is one such region that has long been considered a centre of endemism for many plant and animal species. Similar statements could be made about the Albertine Rift and Madagascar, although to a lesser extent, given the island's isolation. It is therefore crucial to evaluate historical biogeographic hypotheses about African bryophyte diversity using phylogeographic methods.

Taxon-specific trends

It is also important to consider that mosses, liverworts, and hornworts do not follow the same patterns of distribution. Leafy liverworts, for instance, are typically associated with humid, shaded habitats such as bark and foliage. By contrast, many mosses can survive in a wider range of conditions, including xeric rocky outcrops, where several species may have evolved unique adaptations. Finally, complex thalloid liverworts can also be found in Mediterranean climates utilising seasonal rainfall. Hornworts are generally less diverse, and their ecology is less understood. Nevertheless, there is reason

to believe that these plants utilise different resources and occupy different microhabitats. As such, a consideration of all three bryophyte divisions is necessary in any study of this kind. Future research should attempt to separately evaluate richness in leafy liverworts, mosses, and hornworts, as well as various ecological groups such as epiphyllous, corticolous, terricolous, and saxicolous species.

Conservation considerations

The study of bryophyte ecology can directly benefit conservation. First and foremost, it is essential to remember that these plants require specific microclimates to survive. The preservation of forest fragments cannot automatically assume that all habitat needs have been met, since disturbance to the canopy structure can destroy the humid conditions necessary to many bryophyte species. Likewise, the conservation of a mountain or a forest reserve is incomplete without the protection of wet ravines, streams, and peatlands for the epiphytic species that rely on them. In dryland habitats, particular care must be taken to preserve biological soil crusts from destruction by large herbivores and fragmentation by heavy domestic livestock. Conservation planning for bryophytes must therefore go beyond forest conservation to include microhabitat and microclimate stewardship.

The primary recommendation for future research is not to attempt another continent-wide survey, but to formulate standardized observational schemes that can capture large-scale trends. The study should be designed to record richness, abundance, microclimates, and turnover in a consistent manner across different latitudinal and elevational gradients.

Conservation and research priorities

Priority	Reason	Suggested action	Expected output
Afromontane cloud forests	High richness, turnover and sensitivity to humidity	Permanent plots across elevation and canopy strata	Comparable time series of community change
Under-sampled Congo Basin and central Africa	Low confidence in apparent richness deficits	Standardized voucher-based inventories	Improved distribution maps and discovery of overlooked taxa
Sahel and Sahara refugia	Extreme environmental filtering but likely localized diversity	Survey seasonal streams, shaded rock, mountain massifs and ephemeral soils	Baseline data for arid-adapted bryophytes
Madagascar	Island isolation and strong climatic contrasts	Integrate checklist, herbarium and DNA data	Stable taxonomy and better endemism estimates
Cape and Succulent Karoo	Distinct drought-adapted floras and soil-crust communities	Monitor crusts, grazing intensity and rainfall timing	Evidence for disturbance thresholds
Taxonomic infrastructure	Synonymy and cryptic species complicate richness estimates	Support regional herbaria, molecular systematics and training	More reliable species concepts and range estimates
Data integration	Records are scattered among papers and herbaria	Digitize specimens and standardize coordinates and metadata	Continental bryophyte occurrence database

Table 6: Research priorities

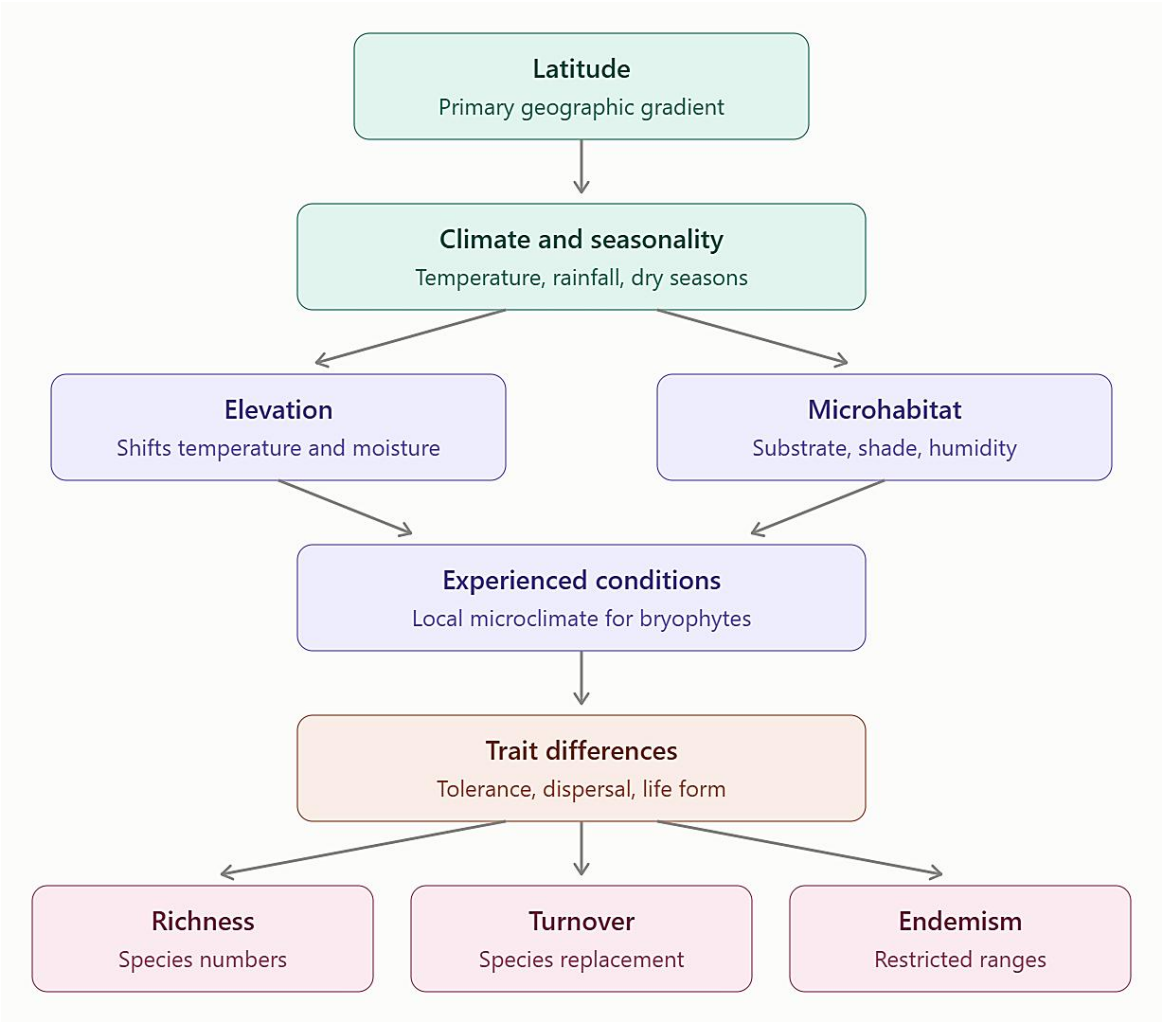

Figure 5: Conceptual pathway linking latitude with bryophyte diversity. Latitude affects climate and seasonality, while elevation and microhabitat modify the conditions actually experienced by bryophytes. Trait differences then influence the observed richness, turnover, and endemism patterns.

6. Limitations and future analytical framework

The greatest limitation of this study is the lack of a standardized continental design. The individual published works that form the basis of this synthesis have used different methodologies, ranging from varying plot sizes to differences in sampling effort and taxonomic resolution. This review therefore focuses on evaluating patterns rather than attempting to create an estimate of continental-scale richness. Another limitation is taxonomy, as new nomenclatural changes can quickly appear and change species concepts. Checklist-based studies should therefore be carefully interpreted as representing a particular moment in taxonomic understanding. In particular, older national flora publications may be significantly at odds with modern molecular phylogenetic research. A third limitation concerns political boundaries. Many national parks and forest reserves contain a wide range of biomes, and a single mountain range or tropical forest area may stretch across multiple countries. Ecological studies should therefore be carried out at levels beyond individual countries. Fourth, the reliance on conceptual maps is also a limitation, as the figures representing this study only aim to demonstrate general trends. Future work should build on this study by analysing digitized herbarium specimen data with particular attention to biogeographic patterns. Researchers should use georeferenced occurrence datasets, apply modern backbone taxonomies, remove duplicates, and quantify sampling effort before fitting spatial models to the data.

Recommended continental analytical design

A future study could use an equal-area continental division to evaluate richness, sampling effort, and taxonomy. Latitude, elevation, precipitation, temperature, vapour pressure deficit, seasonality, vegetation, and conservation status can then be

used as explanatory variables. Likewise, studies concerned with elevational gradients should standardize methods by using consistent transects. Plots should be separated by elevation, and within each plot, ground, rock, tree trunks, branches, leaves, and decaying wood should be sampled. Within each sampled surface, temperature and relative humidity should be measured at the height of bryophyte growth, along with canopy openness, soil or rock pH if applicable, moisture, and exposure. Vouchers should be deposited in major herbarium collections along with the precise coordinates and date of collection.

Molecular methods will be essential to study the patterns of diversity, especially for taxa with limited morphological discrimination. DNA barcoding and phylogenomic methods can help reveal whether diversity recognised at the generic or specific levels corresponds to distinct evolutionary lineages, while also distinguishing between widespread and endemic taxa. Such approaches will provide additional insights into the mechanisms of endemism and help conservation efforts.

7. Conclusions

Based on this review, it is evident that diversity patterns of African bryophytes are indeed closely tied to latitude, but the relationship is best described as complex. The main observed trend was a richness peak near the equator for most bryophyte divisions. However, there were several other centres of diversity that appeared to have more local causes. In particular, moisture, elevation, and habitat heterogeneity often intersected to create exceptionally species-rich habitats. Tropical mountains had an advantage in all three factors and therefore often possessed a wide range of bryophyte communities within a small area.

It is also notable that North Africa and parts of southern Africa can support bryophyte diversity despite the dryness of the climate. This observation highlights the ability of certain plants to utilise the brief rainy season to saturate the local flora with diverse and specialised species. Such an effect can be seen in Mediterranean climates, where winter rains enable bryophyte growth. Thus, the overall latitudinal gradient incorporates several regional variations. However, the greatest challenge in studying the patterns of African bryophyte diversity is the uneven distribution of evidence. Some areas have been thoroughly surveyed and provide a reasonable estimate of taxon richness, while others have few or no records. At the same time, major checklist projects generate hypotheses about diversity that require further testing. This challenge will be addressed when a continental-scale study begins to standardize field surveys, digitize specimens, and utilise modern methods of taxonomy and molecular systematics. In particular, the combination of microhabitat analyses with microclimate studies will be critical to increasing the accuracy of estimations.

A continental understanding of bryophyte diversity will ultimately enable a more nuanced consideration of latitudinal gradients for these plants. Diversity can be structured by latitude, but other variables such as elevation, moisture, and habitat heterogeneity need to be evaluated before making conclusions about biogeographic trends. Lastly, such a study will also highlight the importance of bryophyte conservation for the broader ecological health of Africa's forests, mountains, wetlands, and grasslands.

8. Declarations

Author contributions

The manuscript structure, evidence synthesis, and interpretations were based on the supplied source document and referenced literature.

Data availability

The supporting evidence was based on published literature and checklists. A continental database of occurrences will need to be generated for a future study.

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Appendix A: Suggested standardized field protocol

For a future quantitative continental study, each sampling locality should be described by coordinates, elevation, slope, aspect, vegetation type, canopy openness, substrate class, and recent disturbance history. Sampling should be conducted in at least four substrate classes where present: soil, rock, woody material, and living vascular plant surfaces. In forests, the protocol should distinguish ground, trunk, and canopy strata. At each plot, researchers should record the number of bryophyte taxa observed and the number represented by voucher specimens. Microclimate should be measured at bryophyte height rather than inferred only from a distant weather station. Relative humidity, temperature, substrate moisture, and canopy openness are particularly useful. Sampling should be repeated in wet and dry seasons where feasible. Taxonomic records should use accepted names linked to synonyms. Each voucher should carry a unique identifier and be deposited in a recognized herbarium. Geographic coordinates should be recorded to a precision appropriate for conservation and data-sharing requirements. Rare or threatened taxa should receive additional location protection where necessary.

Appendix B: Recommended tables and figures for a future quantitative version

Output	Minimum variables	Purpose
Continental richness map	Occurrence density, standardized richness, latitude, longitude	Visualize spatial pattern after correcting for effort
Latitudinal curve	Latitude, standardized richness, confidence interval, sampling effort	Test linear, quadratic, and multimodal relationships
Elevation curves	Elevation, richness, humidity, temperature	Separate elevation effects from latitude
Taxonomic comparison	Group, richness, habitat, latitude	Identify divergent moss, liverwort and hornwort responses
Turnover matrix	Site pairs, environmental distance, geographic distance	Test whether elevation and moisture explain beta diversity
Sampling-bias model	Collection count, area, accessibility, habitat coverage	Distinguish research effort from biological richness

Appendix C: Expanded evidence matrix

The matrix below records the principal regional evidence used in the synthesis. It is intentionally descriptive. It does not convert heterogeneous published species lists into a common richness index.

Region/site	Latitude	Main habitat	Bryophyte evidence	Environmental interpretation	Main limitation
Rif and Atlas, Morocco	~30–36°N	Mediterranean woodland, montane forest, gorges	Mediterranean mosses, liverworts and hornworts documented in regional checklists	Winter rainfall, elevation and seasonal moisture permit both drought-tolerant and riparian taxa	Regional checklists combine sites with unequal sampling intensity
Northern Algeria and Tunisia	~30–37°N	Mediterranean forest, maquis, steppe and mountains	Included in Mediterranean annotated checklists	Seasonality and mountain refugia create habitat contrasts	Interior and seasonal habitats remain less consistently sampled
Sahara and Sahel	~15–30°N	Desert, steppe, ephemeral drainage and mountain refugia	Sparse records relative to the size of the region	Water limitation is severe, but localized wet habitats may support specialized taxa	Low sampling prevents strong conclusions about true richness
Ghana and Nigeria forest zones	~4–11°N	Guinean rainforest and forest mosaics	Moss and liverwort checklists document humid-forest taxa	Canopy humidity and substrate diversity support epiphytes and epiphylls	Canopy-level sampling is limited in many inventories
Mount Cameroon	~2–5°N	Lowland rainforest to montane and subalpine habitats	Altitudinal zonation documented by Frahm	Elevation, cloud immersion and temperature structure the assemblage	Older study designs are not directly comparable with modern standardized plots
Bwindi, Uganda	~1–4°N	Afromontane forest	114 species recorded across three forest types	Forest type and elevation influence composition and turnover	Local study should not be extrapolated to national richness
Albertine Rift	~5°N–6°S	Montane forest, volcanoes, highland habitats	Rich liverwort and moss floras reported from several mountain systems	Relief, cloud forest and habitat isolation support turnover	Security and access constrain geographic coverage
Eastern Arc Mountains	~5–10°S	Ancient crystalline mountain blocks, montane forest	Long bryological research tradition and localized taxa	Long-term humid refugia; elevation and isolation are important	Several lowland and coastal sectors remain less sampled
Madagascar, Marojejy	~14–15°S	Humid rainforest and high-elevation habitats	National checklist plus elevational study	Island isolation, rainfall gradient and elevation structure diversity	Taxonomic revision continues to change species boundaries

Region/site	Latitude	Main habitat	Bryophyte evidence	Environmental interpretation	Main limitation
Western and southern Madagascar	~15–25°S	Dry forest and spiny thicket	Seasonal and drought-tolerant taxa documented	Strong seasonality favors desiccation-tolerant life histories	Dry-region bryophytes are less completely surveyed
Zambezian and miombo regions	~10–20°S	Woodland, riverine and inselberg habitats	Fragmented bryological evidence	Local moisture refugia and rock substrates can maintain bryophytes	Large geographic areas lack standardized inventories
Cape Floristic Region	~30–34°S	Fynbos, sandstone ravines, forest patches	Rich regional bryophyte flora in sheltered habitats	Winter rainfall, geology and topographic refugia	Fire and substrate effects complicate broad richness comparisons
Succulent Karoo	~28–34°S	Arid shrubland and soil crusts	Diversity and endemism documented by Hedderson and Zander	Short wet periods and desiccation-tolerant structure assemblages	Long-term recovery and functional-trait datasets are limited