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REVIEW ARTICLE

Bryophytes in the Ecosystem Services: a review

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Abstract

Bryophytes, being one of the most important components of biodiversity, plays important roles in the ecosystem dynamics. They render various services to the ecosystem, such as, formation of soil, providing habitat for small organisms, participation in cycling of nutrients, conservation of soil erosion, control of pests and diseases, bio-monitoring of heavy metals. They are also used as fuel, in horticulture and in construction of houses. They also provide services in cultural aspects as well. However, the information is scattered, and a systematic alignment of these services is still missing to date. Present review brings all the Ecosystem Services (ES) rendered by bryophytes in a single platform, categorized them under the different types of ES as well as identified future areas of research. This review can serve as a catalyst to expand the sphere of cognizance towards classical and new research findings of the ES rendered by bryophytes that can be utilized in conservation, restoration and maintenance of our ecosystem and environment.

Keywords: Bryophytes; Ecosystem Services; Nitrogen Cycle; Nutrient Cycle; Ecosystem Restoration; Soil Conservation; Medicine and Culture

1. Introduction

Human societies share an incredible relationship with the ecosystem. Since time immemorial, human civilizations have been deriving services from the ecosystem (Combertia et al., 2015). These ecosystem services (ES) are "the functions and products of ecosystems that benefit humans, or yield welfare to society" (Millennium Ecosystem Assessment, 2005). The term 'ecosystem services' was coined by Ehrlich and Ehrlich in 1981. However, this concept shot to prominence only in 1997 (Gómez-Baggethun et al., 2010) when ES were highlighted in the literature by Costanza and Daly (1992), Costanza et al (1997) and Daily (1997a, 1977b). The authors emphasized the importance of sustainable use and conservation of ES as well as the ways to estimate their economic value. Since then, it has dominated environmental science and policy literature like a storm (Lelea et al., 2013). Ecosystem services can be grouped into four different categories — provisioning, regulating, supporting and cultural ES (Balvanera et al., 2017). The capacity of the ecosystem to provide goods and services to human society is directly linked with biodiversity (Mori et al., 2017). Biodiversity maintains a broad range of ES, such as climate regulation, food production, pollination, pest control etc. (Cardinale et al., 2012). In this regard, it is worthy to note bryophytes as one of the important components of biodiversity that provide enormous ES. Bryophytes are archegoniate, non-vascular, homosporous simple cryptogams which have no true stem, leaves and roots (Majumdar and Dey, 2020). There are approximately 28,000 species of bryophytes around the globe and constitute the second largest group in the plant kingdom (Shaw et al., 2011). They are present in almost all habitats except sea and oceans and provide significant ES in each of them (Yayintas and Irkin, 2018). Bryophytes are divided into three different phyla, namely, Marchantiophyta (liverworts), Anthocerophyta (hornworts) and Bryophyta (mosses) (Majumdar and Dey, 2020). Bryophytes have a heteromorphic life cycle which includes a short-lived sporophyte that depends on the free-living, leafy gametophyte. These plants can grow on a wide range of habitats providing services, such as initiation of soil formation, control of soil erosion, influencing hydrological and nitrogen cycle, sequestering carbon and indicating the presence of heavy metals in the environment. Besides, they can also provide habitats to microorganisms, provision fuel and construction materials. These may be attributed to the ectohydric, poikilohydric, high capacity to exchange cations and desiccation tolerant nature of bryophytes. These plants also have a high capacity to store water and nutrients. Despite the immense report on the ES rendered by bryophytes, these services are not categorized into the different groups of ES. Thus, it is pertinent to bring all the ES in a single platform and categorize them systematically. In this review article, all the ES rendered by bryophytes are brought in a single platform and categorized under the different types of ES. The article has also identified future areas of research that can aid the understanding of the ES. This review can serve as a catalyst to expand the sphere of cognizance towards classical and new research findings of the ES rendered by bryophytes that can be utilized in conservation, restoration and maintenance of our environment.

2. Ecosystem Services rendered by bryophytes

The types of Ecosystem Services (ES) rendered by bryophytic flora (Figure 1) are fundamentally grouped into the following:

1) Supporting ES: soil formation and vegetation succession, habitat provision, nutrient cycling, carbon cycling and sequestration, nitrogen fixation, restoration of habitat.
2) Regulating ES: regulation of water cycle, soil conservation, pest and disease control, bioindicator of heavy metal.
3) Provisioning ES: provision for fuel, construction materials, green roof, horticulture, clothing, Medicine.
4) Cultural ES: local religious ceremony and rituals, Christmas celebration, body decoration and to ward off evil spirits.

2.1. Supporting Ecosystem Services

2.1.1. Soil formation and succession

Bryophytes play a crucial role in the formation of soil and maintenance of its fertility. They promote soil development by — (i) accelerating physical and chemical weathering: (ii) trapping inorganic and organic material from the atmosphere, and (iii) adding undecomposed organic matter (Vanderpoorten and Goffinet, 2009). Mosses, along with lichens are the first organisms to colonise rocks – rhizoids of bryophytes and rhizines of lichens break up the rock surface, release different organic acids and chelating agents and helped in dissolution of minerals (Porada et al., 2016). In addition, accumulation of death and decay of older parts of mosses on the substratum helps in formation of soil (Majumdar and Dey, 2020).

Bryophytes can inhabit a wide range of substratum, such as volcanic soil, karst areas, bog soil, etc. and promote succession in them. *Nardia succulenta* (Rich. ex Lehm. & Lindenb.) Spreng. a pioneer liverwort can inhabit bare volcanic soil, where along with volcanic ash, forms layered deposits up to 15 cm thick. These deposits then form a continuous carpet by adhering to vertical cliffs and bridges across volcanic boulders and facilitate the initiation of growth of vascular plants (Jongmans et al., 2001). Moss mats can accumulate sufficient moisture and increase fertility, which help in the development of rock loving herbaceous plants, later succeeded by shrubs and trees (Majumdar and Dey, 2020). Bryophytes can also stabilize karst rocky desertification areas and promote vegetation. Along with microorganisms such as fungi and bacteria, they stabilize the physico-chemical properties of surface, create a balanced acidic and alkaline condition, trap dust and nutrients on their substratum, consequently forming soil and promoting establishment and succession of other plant species (Cao et al., 2020).

2.1.2. Habitat provision

Bryophytes provide habitat for a wide range of organisms, such as insects, earthworms, microorganisms, molluscs, nematodes, protozoans, rotifers, spiders, birds as well as other plants (Bahuguna et al., 2013; Glime, 2017d; Glime, 2017e). For small animals and invertebrates, bryophytes provide food, shelter and nesting material. For birds, bryophytes provide a niche for foraging and gathering nest material (Chmielewski and Eppley, 2019). In turn, birds help bryophytes in spore dispersal. Bryophytes also serve as a refuge for the species of order Odonata (e.g, dragonflies and damselflies). Some species like *naiads* use bryophytes as an emergence site where they shed their exoskeleton, leaving it behind as an exuvia (Glime, 2017c). For higher plants, they offer suitable substratum and seed beds for seedling germination (Tavili et al., 2017). Bryophytes also serve as habitats to rare species, for instance, in the United Kingdom, *Heliophanus dampfi* Schenkel, 1923 (Jumping Spider) is found only in Flanders Moss (Stewart, 2001) and two other mires in Wales and Scotland (Harvey et al., 2002). Other species such as *Antistea elegans* Blackwall, 1841, *Arctosa alpigena* Doleschall, 1852 and *Gnaphosa nigerrima* L.Koch, 1877 were found abundantly in bogs but were rare in forest (Glime, 2017f). Bryophytes also establish symbiotic relationships with cyanobacteria and arbuscular mycorrhizal fungi, contributing to N-fixation and P-solubilization (Deane-Coe and Sparks, 2016; Pressel et al., 2021).

2.1.3. Nutrient cycling

Nutrient cycle is a sequence of events consisting of uptake of elements by living organisms from nature, their transfer among organisms and finally, release of these elements back to nature (Yang et al., 2021). Bryophytes have unique twin features of rapid acquisition and slow release of elements back to the environment; thus, they play a significant role in nutrient cycle (Oluwole, 2019). They can mineralize nutrients from the substratum (P) or actively accumulate from the atmosphere and canopy leachates (Ca, K, Mg and N) on their thallus, slowly release these nutrients to soil and make them available for the other plants (Bates, 2009; Alam and Sharma, 2015). In addition, bryophytes also control the flow of nutrients in the environment through biomass production; especially in high latitude and high elevation ecosystems where their dominance is high (Lett et al., 2021). For example, bryophytes contribute more than 50% of the primary production and standing biomass in many tundra ecosystem types (Wielgolaski, 1971; Huemmrich et al., 2010). Also, in black spruce forest, North America, net primary productivity (NPP) of understory (*Sphagnum* dominated) was 51% of the total NPP (understory, overstory, bryophytes and underground) (O'Connell et al., 2003). Therefore, bryophytes act as a primary form of carbon storage in such ecosystems (Singh, 2006) and help in nutrient cycle in the ecosystem.

2.1.4. Carbon sequestration and indication of climate change

One of the most important roles played by bryophytes is sequestration of carbon from the atmosphere. Carbon dioxide (CO_2) is one of the greenhouse gases that warm the earth. Increasing CO_2 in the atmosphere contributes to global warming which is a major threat to the survival of all forms of life. Bryophytes are an efficient CO_2 sequestering agent (Salimi et al., 2021). Hence, they help in mitigation of global warming issues. They regulate carbon budget by absorbing CO_2 from different sources at a rapid pace and trapping them in their biomass due to slow decomposition rate (Smith et al., 2017; Newman et al., 2018; Sun et al., 2017; Vitt and House, 2021). In fact, removal of bryophytes resulted in reduced floor carbon and efflux of mineral soil CO_2, soil organic carbon, microbial biomass carbon and dissolved organic carbon (Sun et al., 2017). In addition, their presence in a wide range of habitats also allows them to influence carbon flux in different ecosystems. Peatlands are one of the ecosystems where bryophytes dominate and play a significant role in sequestration of carbon.

In peatlands (Vitt, 2008), plant biomass production exceeds the decomposition of organic material, and is thus one of the major terrestrial carbon (C) reservoirs. Though they occupy just 2.84% of the land surface, they store 20% of soil carbon present in the world and 60% of the atmospheric carbon (Xu et al., 2018). In fact, they have more carbon storage density per unit ecosystem area than dry terrestrial systems or oceans (Freeman et al., 2012). For example, forested peatlands of eastern Canada accumulated 62–172 kg C m^{-2}, which exceeds the C-accumulation of the above ground tree biomass (1.5–5.3 kg C m^{-2}) (Magnan et al., 2020). The CO_2 concentrating capacity of peatlands can also be increased by adding supplementary phenolic compounds (Alshehri et al., 2020). These compounds are hydrolase enzymes inhibitors, the main decomposing enzyme of soil (Freeman et al., 2001). Consequently, their suppressed activity causes accumulation of organic matter that is sequestered by carbon (Alshehri et al., 2020). The capability of carbon sequestration of peatlands is influenced by various factors such as, level of CO_2 and N_2 in the atmosphere, wildfires, temperature, etc. (Magnan et al., 2020; Serk et al., 2021). Increase of CO_2 in the atmosphere and high-water table enhances C sequestration by promoting biomass production of the plants (Loisel and Yu, 2013; Newman et al., 2018; Serk et al., 2021). On the other hand, increased CO_2 raises the temperature of the atmosphere, which triggers wildfire in the forest causing combustion of superficial layers of peat (Magnan et al., 2020). The intensity of wildfire depends on density, thickness, wetness of surface and varying microforms of peatlands (Benscoter et al., 2011). In addition, higher N in the environment is antagonistic to CO_2 sequestration as it stimulates microbial growth. Microbes enhance decomposition of the organic matter by releasing hydrolytic and oxidative enzymes in surface peat (Bragazza et al., 2012; Larmola et al., 2013).

Carbon sequestration into peat is mainly associated with the bryophyte species *Sphagnum* (also called peat moss), which dominate and form most of the peatlands. In these areas, greater productivity rate and low decomposition rate is conducive for accumulation of thick C rich deposits (Serk et al., 2021). The potential reasons for the slow decomposition rate are (i) *Sphagnum* mosses produce polyphenols which inhibits microbial breakdown (Freeman et al., 2001). *Trans*-sphagnum acid is an important polyphenol unique to peat mosses (Freeman et al., 2012), which is responsible for preservative property of the species, (ii) *Sphagnum* moss have very low concentration of N in their tissue (Aerts et al., 1999) that slows decomposition rate (Vitt and House, 2021). When excess N is supplied to *Sphagnum,* it increases production of cytosolic amino acids by consuming the fixed carbon (Baxter et al., 1992), (iii) *Sphagnum* spp. has high water holding capacity; they can hold 16-26 times its weight in water in both live and dead non-decomposed tissue. This prevents the species from drying out and decomposing due to dry weather conditions, (iv) *Sphagnum* have high cation exchange capacity (CEC) which can make the environment acidic. The uronic acid cell wall of *Sphagnum* contains hydrogen in their carboxylic acid moieties, which get exchanged with base cations present in pore waters. The protons are thus released into the pore waters which subsequently reaches the peatland water, thereby increasing the acidity of peatlands to some extent (Clymo, 1963; Vitt and Weider, 2008), (V) production of organic acids from *Sphagnum* is also a source of acidifying protons in bogs (Vitt, 2008). In addition, conditions such as cool climate with cool moist growing season are favourable for the growth of bryophyte (Smith et al., 2017), which is responsible for accumulation of organic matter over large areas.

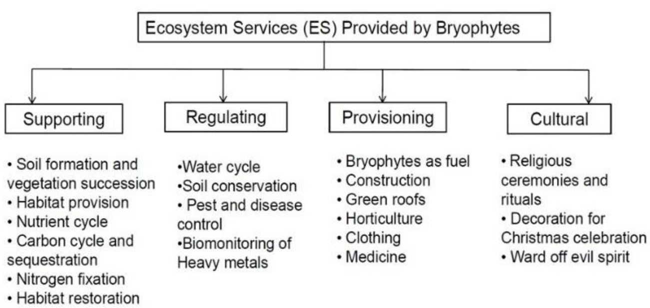

Figure 1. Ecosystem services (ES) rendered by bryophytes. The services are categorised into different groups of ES, namely, supporting, regulating, provisioning and cultural ES.

Bryophytes are also an excellent indicator of climate change owing to their specific ecological requirements and strong affinities to their habitat (Frahm and Klaus, 2001). In bryophyte-dominated ecosystems, species composition and production indicate change in climate (Gignac, 2011). For instance, higher evapotranspiration and less precipitation favours the growth of trees on bogs of Sweden (Gunnarsson et al., 2002). Increasing temperature and extremely dry summer shift the balance between vascular plants and mosses towards higher plants (Malmer et al., 2003). Therefore, by observing the growth and abundance in bryophytes dominated areas, calculating the shift in species' ranges, their interaction with vascular as well as other species of bryophytes, they can be considered as an indicator of climate change (Gignac, 2011).

2.1.5. Nitrogen fixation

In the terrestrial ecosystem, nitrogen (N) is one of the macro-nutrients that limit primary productivity (Ransom et al., 2018; Groffman et al., 2018). Bryophytes help in nitrogen fixation via atmospheric wet or dry deposition, absorption from the substratum, and biological nitrogen fixation (BNF) (Song et al., 2016). Bryophytes form symbiotic association with N_2-fixing cyanobacteria, such as *Nostoc* spp. and diazotrophs (Bay et al., 2013; Berg et al., 2013). In boreal forests, these associations have been shown to fix up to 4 kg N per hectare per year, which is much greater than the amount of N deposited from the atmosphere (Deluca et al., 2007; Deluca et al., 2008; Gundale et al., 2010, 2011). In fact, *Pleurozium schreberi*-cyanobacteria association is estimated to provide N for 80% of the plants covering the floor in boreal forests (Deluca et al., 2007). Moss hosting cyanobacteria (for example, *Fissidens taxifolius* Hedw. and *Thuidium delicatum* (Hedw.) Schimp. hosting *Nostoc* spp.) are also found in other ecosystems such as subarctic tundra and temperate habitats (Deane-Coe and Sparks, 2016; Liu and Rousk, 2022).

BNF is enhanced by optimum moisture, low N_2 concentration in the environment, high P, and warm temperature while suppressed by high N_2 and extreme high or low temperatures Optimum moisture level and low N_2 level encourages cyanobacteria to become active for N acquisition (Zielke et al., 2005; Jackson et al., 2011; Bay et al., 2013; Rousk et al., 2014). This can be seen from the higher N_2 fixation rate in the northern Finland which has low N-deposits (wand lower N_2 fixation rate in Southern Finland which has high N-deposits (Leppänen et al., 2013). High N_2 in the environment suppresses BNF by down regulating cyanobacteria signalling pathways in mosses and negatively affecting nitrogenase activity. High P-levels in the environment show varying results. While it may counter the antagonistic effect of high N_2 on nitrogenase activity (Kox et al., 2016), it can also result in neutral or negative effects on BNF (Rousk et al., 2017). Similar findings were also reported for Mo, a cofactor of nitrogenase activity (Wurzburger et al., 2012). The nitrogenase activity increases in *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Schimp. in boreal forest and subarctic tundra in addition of Mo (10× Mo), suggesting that Mo is a limiting factor for BNF (Rousk et al., 2017; Rousk and Rousk, 2020). However, Scott et al (2018) reported no effect of Mo addition on moss. A gradual rise in temperature increases the bryophyte-associated nitrogenase activity; however, different species show variation in their optimal temperature (Rzepczynska et al., 2022). Under normal temperature, light can impart a positive effect on N_2 Fixation. However, under high temperature, light can cause photodegradation (decreasing pigment and nitrogen concentrations and photosynthetic capacity) to feather moss or cyanobiont as well as impart heat/water stress resulting in low rate of N_2 fixation (Tobias and Niinemets, 2010). In *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Willd. ex Brid.) Mitt. light accompanied with low or intermediate temperatures (16.3, 22.0 ºC) influenced N_2 fixation positively and vice versa when the temperature is high (30.3 ºC) (Gundale et al., 2012). However, Stewart et al (2011) observed that varying light conditions (0-1000 mmol PAR m22 s21) did not affect N_2-fixation rates in *Sphagnum* spp. Accordingly, they suggested that the potential for light to control N_2 fixation rate can be reduced by the stored energy for N_2-fixation and a limited plant canopy (Chapin and Bledsoe, 1992). In addition, forest type and litter leaf input also influence the rate of N_2 fixation (Jean et al., 2020). Till date, N_2 fixation through association with cyanobacteria was mostly studied in *H. splendens* and *P. schreberi* as these mosses are dominant species of the boreal ecosystem. However, other bryophyte species such as *Tomentypnum nitens* (Hedw.) Loeske*, Notothylas* sp.*, Dendroceros* sp.*, Marchantia* sp. and *Porella* sp. etc. are also able to fix N in association with cyanobacteria. Thus, more research involving other bryophytes species and at the molecular level can provide further insight of the topic.

2.1.6 Restoration of habitat

Restoration is the improvement of degraded land or disturbed ecosystems to rebuild ecological integrity and enhance people's lives. Bryophytes are one of the suitable restoration plants in heavily disturbed areas such as post-fire substratum, karst rocky areas, etc. Bryophytes help in restoration of forests by – (i) colonising the substratum. Species like *Funaria hygrometrica* Hedw.*, Ceratodon purpureus* (Hedw.) Brid.*, Marchantia polymorpha* L.*, Bryum argenteum* Hedw.*, Breutelia diffracta* Mitt. can easily colonise the post-fire substratum (Ryoma and Lindberg, 2005; Hylander et al., 2021); (ii) facilitating seedling germination of other plant groups (Rehm et al., 2019). For example, in restoration corridors of *Acacia koa* A.Gray and *Metrosideros polymorpha* J.R.Forst. ex Hook.f., bryophyte mats enhanced seedling germination rate by 10 times as compared to woody litter and nurse logs (Rehm et al., 2019); (iii) they stabilize soil surface, reduce the erosion of topsoil, reduce moisture loss from the soil, improve soil fertility and microbial activity, harbour plant symbionts, such as mycorrhizae and offer free space for germination (Staunch et al., 2012).

Bryophytes help in restoration of Karst rocky desertified areas, as a component of BSCs. Karst rocky deserts are characterized by decrease in soil productivity, wide exposure of basement rocks, and serious soil erosion (Tang et al., 2019). This BSC restores karst area by improving the physical and chemical properties of rock surface, balancing subsoil acidity and alkalinity, by releasing CO_2, carbonic anhydrase, organic acid, and promoting mineral decomposition. It subsequently results in the formation of soil that facilitates invasion and establishment of other plant species, mostly herbs (Zheng et al., 2009; Xiao et al., 2014). Mosses such as *Hypnum leptophyllum* (Schimp.) Boulay, *Hyophila involuta* (Hook.) A.Jaeger, *Racopilum cuspidigerum* (Schwägr.) Ångström are dominant drought resistant bryophyte species found in the Karst rocky desertified area of Guizhou Province, China (Cao et al., 2020).

2.2. Regulating Ecosystem Services

2.2.1. Water Cycle

Bryophytes play important regulatory functions in the water cycle. The ground bryophytes influenced the moisture content and temperature of the soil. In a semiarid climate, mosses increase moisture content of the soil at shallow depth (Xiao et al., 2016). They also help maintain soil homeothermy by evaporation, while returning a large portion of the annual precipitation back to the atmosphere (Chen et al., 2019; Clark, 2019). In the arctic tundra, the thermal–hydraulic properties of moss as well as its organic layer regulate permafrost stability, energy flow and future hydrologic function (Clark, 2019). Bryophytes also take part in water catchment and conservation in forest due to their ability to intercept rainfall (Porada et al., 2018). Bryophytes of Mt. Marsabit forests of northern Kenya trapped eight litres of mist water /m²/ mist day which is equivalent to 196 mm of rainfall per year (Muchura et al., 2014). The hygroscopic capacity of bryophytes is 13% of their own dry weight, which is an additional strength that helps them to harvest water from humid air (Muchura et al., 2014). In tropical montane cloud forest, two liverworts, *Bazzania decrescens* (Lehm. & Lindenb.) Trevis. and *Mastigophora diclados* (Brid. ex F. Weber) captured atmospheric water which is equivalent to 3.46 mm of rainwater (Ah-Peng et al., 2017). These species are ecologically important for the micro-hydrological cycle of the forest, owing to their abundance in the forest; atmospheric water inception, storage and regulated release of water (Ah-Peng et al., 2017). However, these forests are under threat due to anthropogenic effects and climate change (Muchura et al., 2014; Ah-Peng et al., 2017). Therefore, studies on how changing climate will affect bryophytes, their water absorbency and high storage capacity are needed to maintain the hydrological cycle.

2.2.2. Soil conservation

Bryophytes help in conservation of soil by virtue of being a constituent of biocrust or biological soil crusts (BSC) (Warren et al., 2019). BSCs are formed by soil particles in association with a community of organisms including algae, bryophytes, cyanobacteria, fungi and lichens. Initially, the biocrust is dominated by cyanobacteria and algae and within three years bryophytes become the dominant organisms (Seitz et al., 2017).

Bryophytes help in soil conservation by decreasing soil erosion. They shield the soil surface from the impact of raindrops by forming a continuous mat (Figure 2). This mat enhances infiltration as well as surface roughness while decreasing surface runoff (Rodríguez-Caballero et al., 2012). Besides, the rhizoids anchor the soil underneath and prevent it from being eroded (Goebes et al., 2014; Zhao et al., 2014). The ability of bryophytes to prevent soil erosion has been attributed to the following factors (i) the netted webbed protonemata and gametophores that forms a continuous thallus cover the exposed substrata, as well as increase the water holding capacity of the soil to bind the top soil particles (Bahuguna et al., 2013), (ii) they have a rapid regeneration capacity, (iii) they help aggregation of primary soil particles by promoting humus formation (Zhang et al., 2016), (iv) they prevent uprooting of plants by resisting the abrasive forces from both chronic and acute events (v) they can grow in harsh environments (Vitt et al., 2014). In areas prone to landslides, bryophytes are a major agent that prevent soil erosion. Bryophyte dominant crust is more effective in controlling soil erosion than abiotic soil surface such as stones and pebbles because unlike biocrust they cannot influence the hydrological process like surface runoff and infiltration rates (Seizt et al., 2017). A major advantage of BSC is that it can be propagated artificially. Recently, Cheng et al. (2019) successfully cultivated BSC on deserts of north China. Artificially cultivated BSC is low cost and eco-friendly. Therefore, development of artificial BSC should be considered for preventing soil erosion and reforestation (Seitz et al., 2017).

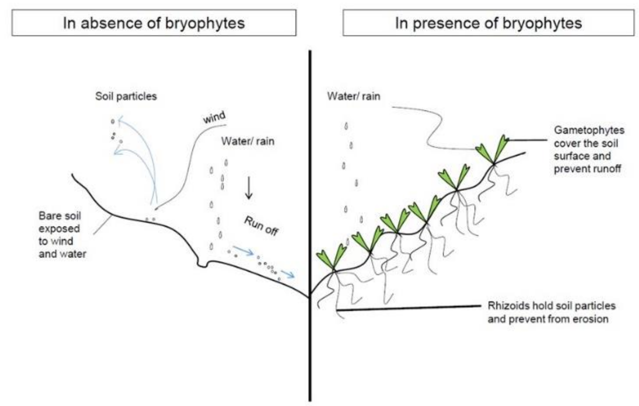

Figure 2. Bryophytes in control of soil erosion. In the absence of bryophytes, the bare soil surface is prone to erosion by rain splash. On the other hand, when bryophytes cover the soil surface, it reduces the impact of rain splash as well as hold soil particles by its rhizoids, thus reducing soil erosion.

2.2.3. Pest and disease control

Bryophytes are endowed with many bioactive compounds including those that can deter pests and disease-causing microbes. Ande et al (2010) reported that application of extracts of *Barbula lambarenensis* P.de la Varde, *Bryum coronatum* Schwagr., *Calympere afzelii* Sw., *Thuidium gratum* (P.Beauv.) A.Jaeger increased mortality of stem borer, reduced their occurrence, recruitment and distribution on the maize plant stands. Fatty acids obtained from *Dicranum scoparium* Hedw., *Hypnum cupressiforme* Hedw., *Homalothecium lutescens* (Hedw.) H.Rob., *Polytrichastrum formosum* (Hedw.) G.L.Sm. and liverworts showed insecticidal activity against *Sitophilus granaries* Linnaeus, 1875 (Chandra et al., 2017). Tadesse et al (2003) reported that ethanolic extracts of *Bazzania trilobata* (L.) Gray, *Diplophyllum albicans* (L.) Dumort., *Dicranodontium denudatum* (Brid.) E.Britton, *Hylocomium splendens* (Hedw.) Schimp., and *Sphagnum quinquefarium* (Lindb.) Warnst. inhibited the growth of *Alternaria solani* Sorauer and *Botrytis cinerea* Pers. by 50%. Methanolic extract of *Funaria hygrometrica* Hedw. reduced biomass in *Alternaria* sp.by 69% (Srivastava, 2015). However, in-depth studies on the bioactive compounds imparting bio-pesticidal activity are still elusive, thus inviting thorough investigations.

2.2.4. Bryophytes as heavy metal bioindicators

Bioindicators are reliable tools used to detect changes in the natural environment (Parmar et al., 2016). It refers to any living organism that can reveal the status of pollutants based on specific symptoms, morphological and anatomical changes and population of species in the ecosystem (Govindapyari et al., 2010; Barkan and Lyanguzova, 2018).

Bryophytes are considered as good bioindicator to assess the atmospheric deposition of metals. Amongst the three different phyla (Marchantiophyta, Anthocerotophyta and Bryophyta), species belonging to Bryophyta are most commonly used as bioindicators of heavy metal pollution and radioisotopes in the air (Oishi and Hiura, 2017; Klos et al., 2018). They are good bioindicator of metals because (i) they are ectohydric and the minerals including heavy metals are adsorbed over the entire surface (Degola et al., 2014) (ii) they can absorb metals easily due to thin cuticle layer (Roberts et al., 2012); (iii) they have prominent ion-exchange properties (Little and Martin, 1974; Clough, 1975); (iv) they have large surface-to-weight ratio (Jiang et al., 2018); (v) they are perennial plants, which can be collected throughout the year (Mahapatra et al., 2019). These factors allow them a faster response to mirror the differences in the level of heavy metals than most vascular plants (Zvereva and Kozlov, 2011). In fact, some of the species of bryophytes are very sensitive to heavy metals and show visible injuries even in the presence of minutest amounts of metals, acting as "warning giver" (Sahu et al., 2007). On the other hand, some species can accumulate metals above their physiological needs and indicate the degree of metal pollution (Miranda et al., 2016). They also offer a simple, easy to handle and cost- effective bioindication technology (Klos et al., 2018). Bryophytes indicate the presence of heavy metals in the environment by reducing the cell size in phyllids, decreasing concentrations of chlorophyll and carotenoids, inhibiting sexual reproduction and increasing death rate (Mahapatra et al., 2019). *Brachythecium rutabulum* (Hedw.) Schimp., *Bryum capillare* Hedw., *B. argenteum* Hedw., *Grimmia pulvinata* (Hedw.) Sm., *Hypnum cupressiforme* Hedw., *Orthotrichum diaphanum* Schrad. ex Brid., *Tortula muralis* Hedw., *Rhynchostegium confertum* (Dicks.) Schimp., *Marchantia polymorpha* L., *Platyhypnidium aquaticum* (A.Jaeger) M.Fleisch., *Rhynchostegium scariosum* (Taylor) A.Jaeger, *Thuidium delicatulum* (Hedw.) Schimp. and *Riccia crassifrons* Spruce indicate the presence of heavy metals by growing vigorously (Govindapyari et al., 2010; Ceschin, 2012; Vasquez et al., 2019). Biomonitoring using moss allows assessment of level of contamination of study areas; sources of origin; and direction of spread of contamination (Klos et al., 2018).

2.3. Provisioning Ecosystem Services

2.3.1. Bryophytes as fuel

Bryophytes, as the major components of peat, are alternative sources of fossil fuels. About half of the annual peat production of the world is for the production of fuels like methane, ethylene, methanol, hydrogen, synthetic or natural gas (Glime, 2007). Peat is a clean-burning fuel and considered a 'slowly renewable energy' by the Intergovernmental Panel on Climate Change (IPCC). *Marchantia polymorpha* L. has a capacity to produce 0.0055 g of lipids per gram fresh weight, thus, can be explored for biofuel production (Sirohi et al., 2019). Recently, *Dicranum montanum* Hedw., a moss, was shown to associate with microbes and generate electricity as bryophyte microbial fuel cells (bryo-MFC) (Hubenova and Mitov, 2011). Bryo-MFC is a carbon-neutral energy conversion technology. Bombelli et al (2016) reported that bryo-MFC using *Physcomitrella patens* (Hedw.) Bruch & Schimp. can generate electrical output which is sufficient to power an environmental sensor or a radio. Bryophytes, along with macroalgae can be a suitable source of third generation biofuel for the future (Sirohi et al., 2019). This suggests an environment friendly and clean fuel being generated from bryophytes. However, as these reports are still at the initial stage, thus, in-depth and rapid pace of investigation is essential to realize the potential of bryophytes in generating fuel.

2.3.2. Construction

Bryophytes are used in construction and furnishing of houses in different regions, especially in countries where mosses are dominant and access to wood is limited (Singh and Srivastava, 2013). In the Himalayan region, moss mats in combination with shrubs, bamboo and grasses are used to make *Pharki*, which is a door placed at the opening of temporary huts (Singh and Srivastava, 2013). Shepherds of the Indian Himalaya used mosses, such as *Actinothuidium hookeri* (Mitt.) Broth., *Anomodon minor* (Hedw.) Lindb., *Entodon* sp., *Floribundaria floribunda* (Dozy & Molk.) M.Fleisch., *Leucodon sciuroides* (Hedw.) Schwägr., *Philonotis* sp., *Thuidium delicatulum* (Hedw.) Schimp., *Plagiochila* sp. as chinking in temporary summer homes (Pant and Tiwari, 1989). Moss species such as *Homalothecium sericeum* (Hedw.) Schimp., *Hylocomium splendens* (Hedw.) Schimp., *Isothecium myosuroides* Brid., *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Racomitrium canescens* (Hedw.) Brid., *Rhytidiadelphus loreus* (Hedw.) Warnst. *and Sphagnum* were used between timbers as chinking in Northern Europe and Alaska (Richardson, 1981; Lewis, 1981). Bryophytes were used to fill spaces between wooden posts of walls and shingles of roofs (Glime, 2007). In Nordic countries, *Fontinalis antipyretica* Hedw. is utilized as fire insulation between the walls and chimney (Thieret, 1956).
Sphagnum moss is a good component to make peatcrete. It is a new, low-cost construction material, which is mouldable into any shape, easy to saw, nail, and is light in weight (Singh and Srivastava, 2013). Peatcrete is made by mixing the *Sphagnum* moss with Portland cement and water (Glime, 2007). The mechanical strength of peatcrete is not very high; however, they are very useful in places which have transportation problems (Glime, 2007).
In remote Polar areas, bryophytes are used in the form of vernacular architecture of extreme climates; however, they are always linked to a secondary role (Glime, 2007). Nowadays, the potential of bryophytes are being recognized as a component of building envelopes. They can be used as substitute for vascular plant in green facades and roofing systems, owing to their capability to colonize different bio-receptivity construction material, high water holding capacity, photosynthetic activity, ability of revival and low maintenance (Garabito et al., 2015; Perini et al., 2020). Incorporating mosses in building envelope/roofing also increases the thermal efficiency of buildings (Garabito et al., 2015). Perini et al. (2020) also reported that moss can be an interesting and affordable alternative green envelope for a large-scale production. Therefore, important steps should be taken to disseminate the usefulness of bryophytes as a building material, to both the developed and developing countries. It will be a small but a very crucial step to balance the conflict between development and environment.

2.3.3. Green roofs

A green roof is a layer of vegetation planted on a building over a waterproofing system. It is particularly popular in urban areas, as it helps in — (i) cleaning the atmosphere, (ii) buffering the temperature, (iii) reducing roof run off, (iv) fireproofing, (v) creating sound proof barrier (Glime, 2017g), (vi) reducing urban heat island effect (Razzaghmanesh et al., 2016), (vii) improving urban wildlife habitat where different species of avifauna, invertebrates and other small organism can survive (Mayrand and Clergeau, 2018) and (viii) storm water retention with better water quality (Razzaghmanesh et al., 2014). In this regard, bryophytes serve as a useful substrate for green roofs. Ecologists have proved that mosses and lichens improved green infrastructure properties and green roofs (Heim and Lundholm, 2014; Heim et al., 2014). Benefits of using bryophytes (mainly mosses) as green roof includes (i) ability to survive and grow in harsh condition like that of roof, (ii) resistance to drought owing to poikilohydric nature, (iii) smaller weight and less requirements of substrate quantity and quality (Studlar and Peck, 2009; Heim et al., 2014), (iv) no need of addition of fertilizer, (v) need less maintenance and is cost effective compare to other kinds of green roof vegetation (Glime, 2017g; Martin, 2015). Species like *Bryum argenteum* Hedw., *Tortella nitida* (Lindb.) Broth. and *Trichostomum crispulum* Bruch, *Tortula muralis* Hedw., *Didymodon fallax* (Hedw.) R.H.Zander, *Grimmia lisae* De Not., *Syntrichia laevipila* Brid., *Ceratodon purpureus* (Hedw.) Brid., *Pleurochaete squarrosa* (Brid.) Lindb. and *Tortula inermis* (Brid.) Mont. are identified as most suitable bryophytes for green roofing (Cruz de Carvalho et al., 2019). Out of which, *C. purpureus* is the best candidate to be introduced as green roof vegetation (Burszta-Adamiak et al., 2019). However, the lack of awareness of their potential utility and efficient local production are upsetting the use of mosses in green roofing. Therefore, more efforts are needed to create awareness to the common people about the benefits these small plants can give us.

2.3.4. Horticulture

Bryophytes have been used in horticulture for a very long time. They are being used as soil conditioner, seed beds, moss garden, culturing and cultivation of mushroom, air layering, pot culture, development of bonsai and bonkei plants etc. (Alam and Sharma, 2015). This may be attributable to the bryophytes' ability to increase nutrient status, water holding capacity, permeability of air, cation exchange capacity and aggregation of soil particles (Mahrup et al., 2019). Mosses such as *Polytrichum juniperinum* Hedw. and *Pleurozium schreberi* (Willd. ex Brid.) Mitt. enhanced seedling germination in *Picea mariana* Britton, Sterns & Poggenb. (Mallik and Kayes, 2018). Moss species like *Camptothecium arenarium* (Lesq.) A.Jaeger, *Hypnum imponens* Hedw., *Leucobryum* spp, *Rhytidiopsis robusta* (Hook.) Broth., and *Thuidium delicatulum* (Hedw.) Schimp. are preferred substrates for growing ornamental pteridophytes and orchid plants. *Sphagnum* spp. are useful in culturing mushroom *Agaricus bisporus* (J.E.Lange) Imbach and other fungi (Beyer, 1997). The species is also crucial for air-layering methods for propagation of plants (Macdonald et al., 1995). Furthermore, in bonsai and bonkei plants development, mosses help to stabilize soil and retain moisture, providing a warming system when delicate dwarf plants need water (Saxena and Harinder, 2004).

In recent times, moss gardens are becoming very popular in Japan, USA, UK, Canada. India developed its first moss garden in Uttarakhand in 2020. The garden not only adds aesthetic value but also provides numerous ecosystem services. They can convert a barren area into a green cover without addition of fertilizers; their tissues contain secondary metabolites that acts as natural pesticides and herbicides; water usage and maintenance is lower in comparison to traditional lawns; they provide microhabitat for beneficial insects, salamanders and other organisms; they also absorb a lot of harmful toxins keeping the area clean (Martin, 2015; Glime, 2017b).

2.3.5. Clothing

Bryophytes were used in clothing and attires in different parts of the world. In Germany, *Sphagnum* moss was used with wool or thread to make cheap and good quality cloth (Hotson, 1921). In Mexico, a rock inhabiting moss was used to colour wool with their dark coloured extracts (Glime, 2007). Mosses species like *Spiridens reinwardtii* Nees, *Climacium dendroides* (Hedw.) F.Weber & D.Mohr, *Dicranum* sp., *Dawsonia* sp. were used to decorate lady's hat, bonnet and body wears by women of Phillipines, England, Papua New Guinea (Tripp, 1888; Dickson, 2000; Tan, 2003). In New Guinea, *Dawsonia grandis* Geh. were used to decorate bracelets. Leaves of the species were also plaited with red rope for decoration of net bags (Zanten, 1973). In New Zealand, *Polytrichadelphus magellanicus* (Hedw.) Mitt. and *Polytrichum commune* Hedw. were used to decorate Maori cloaks (Beever and Gresson, 1995). In Germany and Nordic countries, *Sphagnum* sp. was popularly used to line hiking boots as it helps in cushioning the feet, absorbing moisture and odours and in discouraging bacteria as well. Dickson et al (1996) reported that 30 species of bryophytes were used in Tyrolean Iceman's clothes. Most common species were *Polytrichum piliferum* Hedw, *Pohlia* spp., *Andreaea* spp., *Racomitrium lanuginosum* (Hedw.) Brid. *and Polytrichastrum sexangulare* (Flörke ex Brid.) G.L.Sm.

Bryophytes have long been used as diapers in several cultures. In Aboriginal societies, peat moss with animal skin covering was used as diapers to absorb urine (Glime, 2017h). In fact, the famous modern company Johnson and Johnson used *Sphagnum* for lining diapers and in sanitary napkins (Gottesfeld and Vitt, 1996). *Sphagnum* moss absorbs water from skin and prevents diaper rash just like the talcum powder. The species also helps to remove baby's faeces from the skin easily (Elliott, 2012). However, the discoloured moss should be avoided as it may be affected by fungus *Sporothrix schenckii* Hektoen & C.F.Perkins, which causes sporotrichosis (Glime, 2017h). These activities demonstrate that bryophytes have potential to be used for clothing. However, most of the uses are traditional. More research can be directed towards the development of the traditional uses in a modern way.

2.3.6. Medicinal uses of bryophytes

The use of bryophytes in traditional and modern medicines is well documented. In India, people of the Himalayan region used ashes of mosses mixed with honey and fats as ointment for burns, wounds and cuts (Saxena and Harinder, 2004). In China, *Marchantia polymorpha* L. has been used as medicine for treating hepatic disorders, boils and abscesses (Glime, 2017a; Mossang et al., 2021). Harris (2008) also provided data on the traditional medicinal usage of various bryophyte species.

In modern medicines, bryophytes are used for treatment of various diseases, such as, bacterial, fungal, cancer, diabetes, arthritis, cardio-vascular diseases (Ludwiczuk and Asakawa, 2019, Mossang et al., 2021). The medicinal properties of bryophytes are attributed to the presence of numerous compounds such as proteins, carbohydrates, lipids, polyphenols, terpenes, steroids, fatty acids, organic acids, sugar, aromatic and aliphatic compounds, alcohols, acetogenins, phenolic substances and phenyl quinines (Halder and Mitra, 2020). Some medicinally important bryophytes are *Marchantia* sp., *Calymperes motley* Mitt., *Fissidens* sp., *Hypnum cupressiforme* Hedw., *Plagiochila* spp., *Sematophyllum demissum* (Wilson) Mitt., *Conocephalum conicum* (L.) Underw., *Octoblepharum albidum* Hedw., *Bryum capillare* Hedw., *Marchantia convolute* C.Gao & G.C.Zhang, *Porella* sp., etc. Recently, a drug from the moss, *Physcomitrella patens* (Hedw.) Bruch & Schimp., has successfully completed the first stage of its clinical trial for treating a genetic disease called Morbus Fabry (Decker and Reski, 2020). However, despite the importance of bryophytes medicinally, phytochemical studies of bryophytes are still scanty in comparison to vascular plants, thus calling for in-depth investigation from the scientific community.

2.4. Cultural importance of bryophytes

In countries like China, India, the United States and Canada, bryophytes were used in cultural activities. Species such as, *Bryum* sp., *Chiloscyphus orizabensis* Gottsche, *Dendropogonella rufescens* (Schimp.) E.Britton, *Meteorium* sp., *Polytrichum* sp. and *Thuidium* sp. were used for religious ceremonies and rituals in different parts of Mexico (Martinez-Lopez et al., 2017; Hernandez-Rodriguez and Delgadillo-Moya, 2020). In Christmas, *Squamidium* sp., *Bryum procerum* Schimp., *Dicranum* spp., *Braunia* sp., *Hypnum amabile* (Mitt.) Hampe, *Pilotrichella flexilis* (Hedw.) Ångström, *Campylopus* spp., *Polytrichum* spp., *Leptodontium* sp., *Mironia ehrenbergiana* (Müll.Hal.) R.H.Zander, *Pterobryon densum* Hornsch., *Thuidium delicatulum* (Hedw.) Schimp. were used for decoration. In Malaysia, *Spiridens* spp. were used to decorate body and to ward off evil spirits (Glime, 2017h).

3. Future perspectives and conclusion

Bryophytes as an ecologically important group of plants is unparalleled and the Ecosystem Services they render is of immense importance. However, this group of plants has not been explored fully to derive optimum benefits from them. Therefore, future research can be directed towards bridging the major gaps highlighted. Bryophytes are found to be well associated with N_2–fixing cyanobacteria. However, this association has not been explored beyond the arctic and subarctic regions. Thus, more studies are needed to unravel the potential of this association to derive maximum benefits. The role of bryophytes in tolerating heavy metals stress is well studied. However, a small percentage of bryophytes species were reported. Hence, the heavy metal tolerance capacity of more species can be explored. Including molecular studies can fill major gaps in understanding the mechanisms of tolerance. Bryophytes have the potential for production of fuel. Bryo-MFCs can be investigated further to obtain maximum utilization of this clean technology. Out of approximately 28,000 species of bryophytes present in the world, only 1000 species have been used for therapeutic studies. There is a lot of scope of finding more useful bryophyte species for medicinal and cultural purposes.

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Authors contributions

HE conceptualized the topic and all the authors contributed equally to the preparation of the manuscript.

Conflict of interest

The authors declare that there is no conflict of interest.

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