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A research agenda for nonvascular photoautotrophs under climate change

Summary

Nonvascular photoautotrophs (NVP), including bryophytes, lichens, terrestrial algae, and cyanobacteria, are increasingly recognized as being essential to ecosystem functioning in many regions of the world. Current research suggests that climate change may pose a substantial threat to NVP, but the extent to which this will affect the associated ecosystem functions and services is highly uncertain. Here, we propose a research agenda to address this urgent question, focusing on physiological and ecological processes that link NVP to ecosystem functions while also taking into account the substantial taxonomic diversity across multiple ecosystem types. Accordingly, we developed a new categorization scheme, based on microclimatic gradients, which simplifies the high physiological and morphological diversity of NVP and world-wide distribution with respect to several broad habitat types. We found that habitat-specific ecosystem functions of NVP will likely be substantially affected by climate change, and more quantitative process understanding is required on: (1) potential for acclimation; (2) response to elevated CO_2; (3) role of the microbiome; and (4) feedback to (micro)climate. We suggest an integrative approach of innovative, multimethod laboratory and field experiments and ecophysiological modelling, for which sustained scientific collaboration on NVP research will be essential.

Introduction

Nonvascular photoautotrophs (NVP) include organisms of old lineage, such as bryophytes (mosses, liverworts, and hornworts), lichens, terrestrial algae, and cyanobacteria, which are all characterized by their lack of vascular tissue. Without roots, NVP cannot access water within the bulk soil and depend on direct uptake of water from the atmosphere in the form of rainfall, dew, fog, and water vapor, or contained in the near-surface layer of the substratum. Due to the lack of active control on water loss, the organisms frequently dry out. In contrast to most vascular plants, however, they are able to substantially adapt their metabolism to this large variation in their water content, which allows them to thrive in epiphytic and lithic habitats without direct contact with soil water. They are abundant world-wide, and communities of NVP may even represent the dominant form of vegetation in many ecosystems with limited water availability, such as deserts, tundra, and at high elevations.

Nonvascular photoautotrophs have been suggested to perform key processes in various ecosystems at the global scale (Fig. 1). Mosses growing on the forest floor, for instance, may contribute *c.* 50% to ecosystem nitrogen input via their association with nitrogen-fixing bacteria (DeLuca *et al.*, 2002). Epiphytic NVP in forests may increase rainfall interception by > 60%, thus influencing precipitation partitioning, that is, the division of rainfall into different pathways, such as throughfall, stemflow, and evaporation, that ultimately return water to the atmosphere. This also affects near-surface air temperature and plant available water (Porada *et al.*, 2018). Mosses contribute up to 50% of the aboveground net primary productivity (Turetsky *et al.*, 2012) in high-latitude peatland ecosystems that are estimated to store 30% of global soil carbon (Yu *et al.*, 2010). In drylands, NVP form the major part of biological soil crusts (biocrusts) that play a crucial role for ecosystem carbon and nutrient cycling (Rodríguez-Caballero *et al.*, 2018a). Furthermore, biocrusts have been shown to protect the soil surface against erosion by water (Seitz *et al.*, 2017) and wind (Duniway *et al.*, 2019) and regulate soil water content (Eldridge *et al.*, 2020). In addition to biogeochemical cycles of carbon, nutrients, and water, NVP may have substantial biogeophysical effects on ecosystems, such as impacts on albedo and soil temperature (Bernier *et al.*, 2011; Couradeau *et al.*, 2016). At high latitudes, insulation by mosses and lichens may cool the soil by > 2°C, thus protecting permafrost carbon (Porada *et al.*, 2016). Additionally, NVP play key roles in food webs and successional processes in multiple ecosystems (Asplund & Wardle, 2017; Lett *et al.*, 2017).

Nonvascular photoautotrophs and their role in ecosystem processes and services may be seriously affected by climate change (Reed *et al.*, 2012; Sancho *et al.*, 2017; Rodríguez-Caballero *et al.*, 2018a). Multiple studies suggest negative impacts of warmer, drier air on the growth of NVP (e.g. Nascimbene *et al.*, 2016; Ladrón de Guevara *et al.*, 2018; Norby *et al.*, 2019; Finger-Higgens *et al.*, 2022). Moreover, indirect effects, such as increased competition with vascular plants, may further reduce NVP cover, especially in the Arctic tundra and in high-elevation ecosystems (Cornelissen *et al.*, 2001). In general, however, it is uncertain how NVP will respond to climate change over the next decades, though, as noted earlier, the response could have major consequences for the biosphere. In particular, it is not known to what extent potential changes in the composition of NVP communities will alter ecosystem functions. In contrast to vascular plants, NVP have been underappreciated by the wider scientific community as a relevant source of ecosystem services, including climate regulation at the global scale (Rodríguez-Caballero *et al.*, 2018b).

This article aims at promoting urgently required research, which is necessary to better understand the responses of NVP to climate

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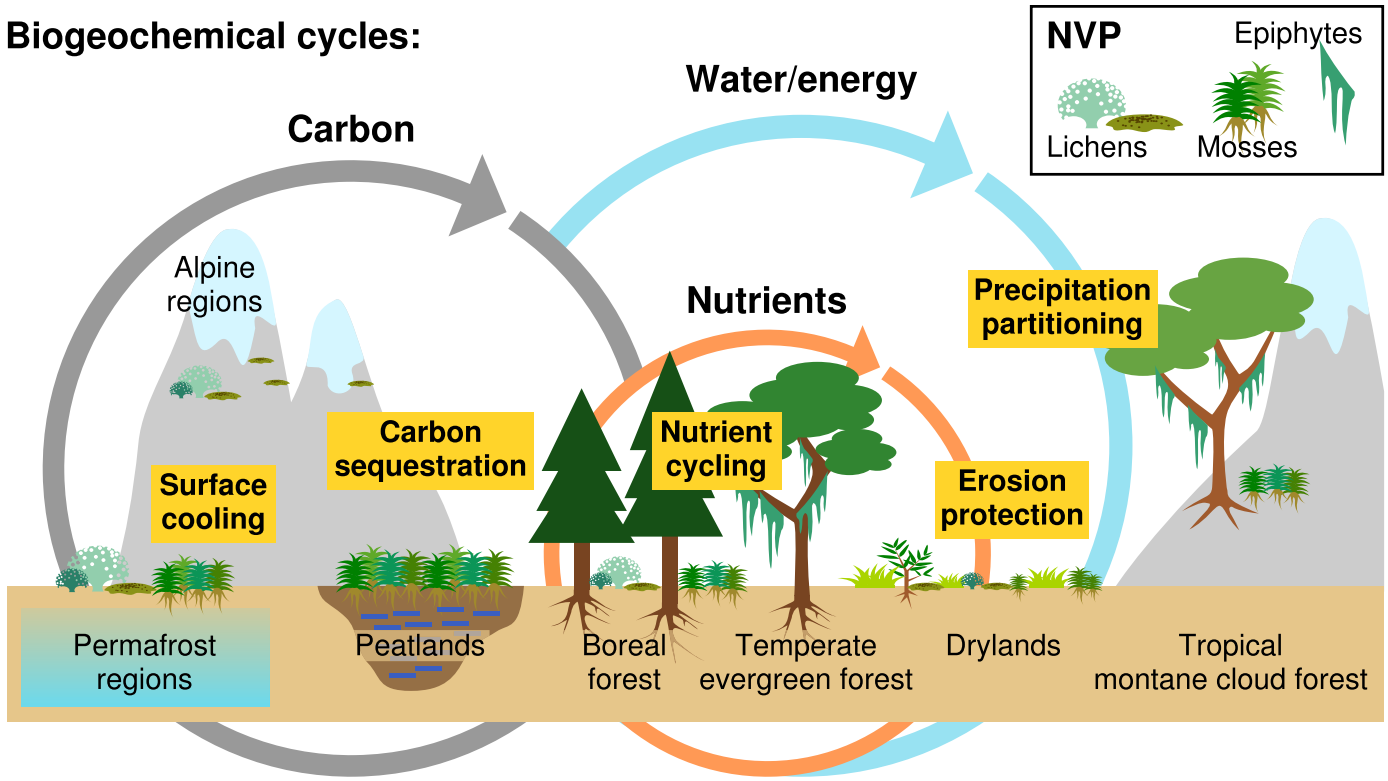


Fig. 1 Impacts of nonvascular photoautotrophs (NVP) on key aspects of ecosystem functioning (yellow boxes) in selected ecosystem types that show a high abundance of NVP. The effects are categorized according to the interconnected biogeochemical cycles of carbon (grey arrow), nutrients (mainly nitrogen and phosphorus) (orange arrow), and water and energy (blue arrow). The cycles are arranged according to the supposed primary impacts of NVP in the respective ecosystems. These impacts are, however, not limited to a specific ecosystem.

change and the associated potential consequences for their ecosystem functions and services. As we focus on photoautotrophs, other organisms that live together with NVP in cryptogamic communities, such as (associated) heterotrophic microbes, are not explicitly considered here. These organisms may also differ from NVP regarding their response to climate change.

We assess knowledge gaps on *overarching climate response mechanisms that apply to a large range of NVP in multiple ecosystems*. The analysis of these general response patterns is complicated by large intra and interspecific variations of NVP with regard to physiological and morphological traits and a wide range of environmental conditions in habitats of NVP. Therefore, we introduce here a new framework for the categorization of habitat types along microclimatic gradients. This broad concept helps to identify potential general relations between climate and traits of NVP, and it may provide indications for the reaction of NVP to changes in climate.

Categorization of nonvascular habitat types along microclimatic gradients

Nonvascular photoautotrophs occur over a wide range of climatic conditions in almost all ecosystems of the world (see Fig. 1). Their growth depends mostly on local microclimate, which may differ substantially from climate at a larger scale (Raggio *et al.*, 2017; Colesie *et al.*, 2018). To clarify the links between microclimate, community structure of NVP, and ecosystem functioning across various regions of the world, we propose here a scheme for the categorization of nonvascular habitat types along three microclimatic gradients, thereby also considering climatic variability (see also Fig. 2): (1) ambient temperature during activity, which may differ from diel and annual mean temperature. When NVP are dormant, temperature does not have a large influence on their metabolism (Proctor, 2000); (2) water availability, which may result from high relative air humidity, dew, fog, hoarfrost, direct rainfall or throughfall and stemflow (Gauslaa, 2014), snow melt, or capillary rise in wetlands and additionally depends on environmental structures, for example, canopies or topography. Thus, water availability may differ markedly from rainfall pattern and intensity; (3) light availability during activity, which is influenced by cloud cover and fog (Gotsch *et al.*, 2016), light transmission under heterogeneous plant canopies, snow cover (Pannewitz *et al.*, 2003), or even mineral layers in case of endo and hypolithic NVP (Weber *et al.*, 2011). Our scheme also considers *climatic variability*, because any habitat type, defined by given temperature, water, and light availability, may be further differentiated into regions of high, medium, and low variability. We thereby integrate over diurnal, seasonal, and interannual variability of one or more of the microclimatic factors (Fig. 2).

We identified four broad habitat types: *open ground* surface (which also includes rock surfaces), *peatlands*, forest *understory*, and

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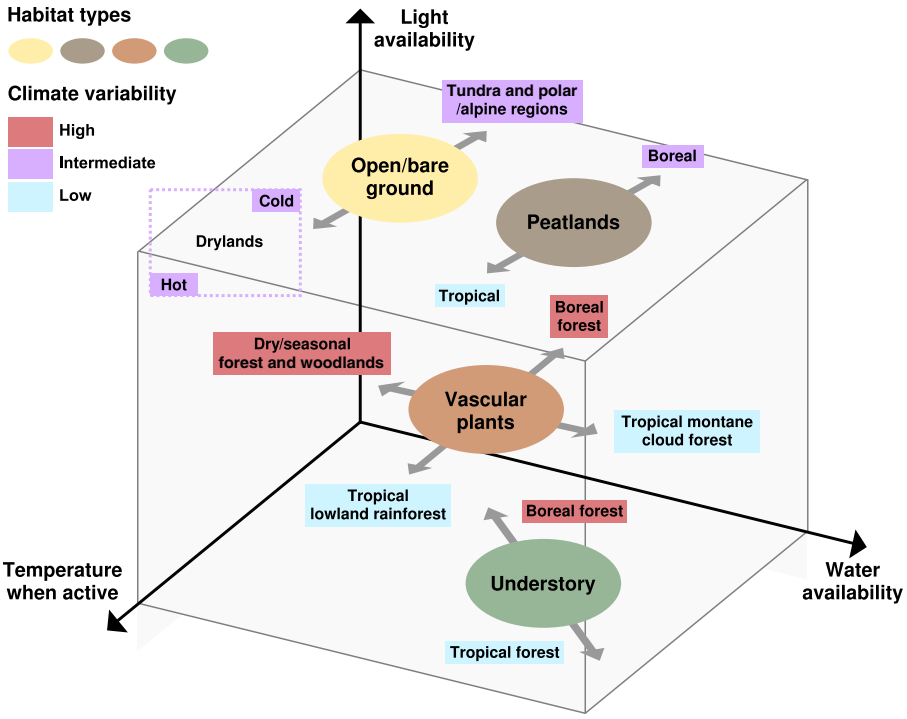


Fig. 2 Categorization of four habitat types (ellipses) of nonvascular photoautotrophs along three microclimatic gradients. The habitat types are further subdivided along the gradients (example ecosystem types shown in boxes) and additionally exhibit different degrees of climate variability (color of the boxes denotes low to high variability from blue to red, integrating from diurnal to interannual time scales).

vascular plants (trees or shrubs, for epiphytes). These habitat types still contain marked variation with regard to climatic factors and the physiological or morphological traits of NVP. However, we expect that they suitably differentiate key ecosystem functions and services of NVP and help to define broad physiological strategies showing a consistent response to climate change. As global warming is related to the increase in atmospheric CO_2 concentration, we also include in our analysis CO_2 as a factor that affects the growth of NVP. Our categorization scheme may be later extended by further dimensions to account for nonclimatic effects on NVP distribution, function, and services.

Potential impacts of climate change on key ecosystem functions of NVP

Climate change effects are distributed unevenly over the global land surface (Arias *et al.*, 2021). While increased atmospheric CO_2 concentration shows a relatively uniform pattern, polar regions exhibit a two- to threefold higher warming than mid-to-low latitudes. Changes in precipitation patterns are less well understood, but are expected to be more complex, with increases at high latitudes and in several tropical regions and decreases at mid-latitudes. This may be accompanied by reductions in relative humidity. Moreover, climatic variability is expected to increase, resulting in more frequent extreme events, such as droughts, heat waves, heavy rainfall, and wildfires. While overarching patterns likely exist, we expect the climate response of NVP and associated changes in ecosystem functions to differ on average between the four broad habitat types that we have identified here (see also Table 1). Therefore, we sort our findings accordingly into four categories.

Open ground

Key ecosystem functions of NVP on open ground vary between ecosystem types, leading to differential impacts of climate change. In drylands, warming experiments suggest negative effects on cover and diversity of biocrusts, likely due to reduced active time resulting from drier and warmer air and also higher respiration (Maestre *et al.*, 2013; Ladrón de Guevara *et al.*, 2018; Baldauf *et al.*, 2021), which, however, may depend on the type of biocrust (Tucker *et al.*, 2019; Li *et al.*, 2021). The negative effects of warming may be exacerbated by a shift in climate variability, such as a higher number of small rainfall events, which may cause high carbon losses through maintenance respiration (Reed *et al.*, 2012; Phillips *et al.*, 2022). These results are consistent with estimates of decreased biocrust cover based on large-scale statistical modelling (Rodríguez-Caballero *et al.*, 2018a). Cover reduction, but also a shift in species composition, may lead to increased susceptibility of the soil surface to erosion by wind and water (Eldridge *et al.*, 2020) and also enforce a feedback between surface albedo and climate (Rutherford *et al.*, 2017). In addition, substantial alteration of ecosystem nitrogen fixation and carbon sequestration may occur (current contributions by NVP of 25% and 10% on average, respectively; Elbert *et al.*, 2012; Rousk & Michelsen, 2017), and also phosphorus cycling may be affected (Concostrina-Zubiri *et al.*, 2022; García-Velázquez *et al.*, 2022). Furthermore, climate change impacts on NVP-mediated soil nutrient cycling will likely be species-specific (Concostrina-Zubiri *et al.*, 2021).

At high latitudes, effects of climate change on NVP may lead to a modulation of the positive feedback between global warming and carbon emissions from permafrost soils through changes in the capacity of mosses and lichens to cool the soil surface (Bernier

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Table 1 Negative impacts of climate change on main ecosystem functions and services of nonvascular photoautotrophs (NVP) per habitat type, associated functional types of NVP, main potential impact factors of climate change, and key knowledge gaps in this regard (see text for references).

Habitat type	Characteristic functional type	Main climate impact factors	Ecosystem functions affected by climate change	Key knowledge gaps
Open ground	Cyanobacteria, dryland/ tundra Lichens, and bryophytes	Temperature, relative humidity, Precipitation variability	Erosion protection, ground cooling, nutrient cycling	CO_2 fertilization, acclimation potential, competition, symbiotic relations
Peatland	Peat moss	Temperature, extreme weather	Carbon sequestration	Nutrient limitation, microbiome effects
Understory	Bryophyte (and lichen) carpets	Temperature, rainfall variability, light availability	Nutrient cycling, precipitation partitioning, carbon sequestration	Symbiotic relations, microbiome effects, acclimation potential
Vascular plants	Bryophytes and lichens	Temperature, light availability, rainfall variability	Precipitation partitioning, temperature regulation	Community turnover, acclimation potential, climate feedbacks

et al., 2011; Porada *et al.*, 2016). In the Northern Hemisphere, whether warming and changes in rainfall patterns will have an overall positive or negative effect on NVP is not clear (Deane-Coe *et al.*, 2015). This is complicated by uncertainties in the response of vascular high-latitude vegetation to climate change (Myers-Smith *et al.*, 2020), which will likely modulate microclimatic conditions for NVP.

In alpine regions, and also in deserts, changes in climate may affect epilithic and endolithic NVP, with consequences for local weathering rates (Weber *et al.*, 2011). At high elevations, snow melt will be faster and in late summer, less melt water will be available for high-alpine moss and lichen communities (Scheidegger, 2021). Little quantitative knowledge exists in this regard, but impacts on biogeochemical cycling may be substantial, because NVP may represent the dominant vegetation in these habitats.

Peatlands

Climate change is expected to affect the productivity of NVP in peatlands, particularly at high latitudes. Nonvascular photoautotrophs contribute substantially to carbon sequestration via input of dead biomass under anoxic conditions (Street *et al.*, 2013; Weston *et al.*, 2015). This is enhanced by the release of phenolic compounds and acids from NVP, which impede microbial decomposition of organic matter (Dieleman *et al.*, 2017). While warming may extend the growing season at high latitudes, weather extremes such as heat waves, associated with water table drawdown, changes in rainfall patterns, and increased fire risks may have strong negative effects on NVP (Loisel *et al.*, 2021). Moreover, warmer climatic conditions and increased nitrogen availability may lead to increased cover of vascular plants, altering the microclimate for NVP (Malmer *et al.*, 1994). The potential changes in peatland hydrology may substantially increase emissions of CO_2, CH_4, and N_2O from these ecosystems in the next decades, due to enhanced microbial activity under oxygenated and warmer soil conditions, particularly in permafrost regions (Hugelius *et al.*, 2020).

As it is not completely clear which factors limit the growth of NVP in peatlands, potential effects of climate change on NVP remain uncertain. Several studies suggest nutrient limitation of productivity in these ecosystems, regarding nitrogen, phosphorus, or both (Aerts *et al.*, 1992). This may lead to a marked reduction in a potential CO_2 fertilization effect in the future (see also 'All habitat types' in the Potential impacts of climate change on key ecosystem functions of NVP section). Furthermore, the ability of different species of peat mosses (*Sphagnum*) for coping with warmer and drier conditions needs to be better examined, in particular the role of the organisms' microbiome (Carrell *et al.*, 2019).

Understory

A dense layer of NVP on the ground is not only a feature of boreal forests, but may also occur in temperate (rain) forests (Berdugo *et al.*, 2018), and tropical montane cloud forests (Rodríguez-Quiel *et al.*, 2019). A key ecosystem function of NVP in the forest understory that will likely be affected by climate change is the biotic fixation of nitrogen through associated microbes (DeLuca *et al.*, 2002), because the magnitude of this process strongly depends on the water content and temperature of NVP (Rousk *et al.*, 2018). In addition to these direct effects, climate-induced shifts in forest type, also due to changes in local fire regime, may modify microclimate, including light availability, and have impacts on NVP and biotic nitrogen fixation (Lindo *et al.*, 2013). Other relevant ecosystem functions governed by understory NVP that may be affected by climate change include storage and evaporation (up to 50%) of net rainfall (Porada *et al.*, 2018) and input of carbon into the soil (Street *et al.*, 2013).

As biotic nitrogen fixation associated with NVP is spatially heterogeneous and highly dynamic, it is challenging to assess future changes based on current knowledge from short-term site-level measurements (Salazar *et al.*, 2020). Furthermore, the nature of the relationship between microbes and NVP is not entirely clear. While it is established that cyanolichens represent a symbiosis between a fungus and a cyanobacterium, it is not known to what extent mosses benefit from the presence of nitrogen-fixing microbes and *vice versa* (Rousk *et al.*, 2013). Effects of altered temperature and moisture supply due to climate change may thus also depend on the reaction of the microbiome, and not only on the response of the plant.

Vascular plants

Climate change is expected to negatively affect epiphytic and epiphyllic NVP, that is, growing on the bark of trees and shrubs or

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on leaves across various forest ecosystems (Ellis, 2013). Epiphytes have been shown to intercept substantial amounts of rainfall and fog (Van Stan II & Pypker, 2015). The subsequent evaporation reduces soil water availability for vascular plants and also cools the canopy (Davies-Barnard *et al.*, 2014). Hence, key consequences for ecosystem functioning following the potential reduction in NVP will likely include alterations to net precipitation below the canopy and to energy and water balances in the canopy. Additionally, nutrient cycling may be affected due to the substantial role of NVP for nitrogen inputs in some forests (Clark *et al.*, 1998), and also the formation of canopy soils (Gotsch *et al.*, 2016) may be affected with consequences for other canopy organisms such as vascular epiphytes and invertebrates.

While some species may benefit from warmer conditions, many studies suggest negative consequences of climate change for epiphytic NVP, in particular in case of more frequent extreme drying events (Nascimbene *et al.*, 2016; Smith *et al.*, 2018). Warming and drying may reduce active time and/or cause increased respiration costs, but also warming accompanied by prolonged water saturation may lead to higher respiration (Ellis, 2019a; Metcalfe & Ahlstrand, 2019).

Major uncertainties exist regarding the extent to which the function of NVP could be stabilized by community turnover in response to reduced availability of water or shifts in the water source, such as rainfall, dew, or fog (Rubio-Salcedo *et al.*, 2017). If these changes in community composition reduced the average water storage capacity of the organisms or their water uptake efficiency (Hovind *et al.*, 2020), this may lead to a positive feedback on increased canopy temperature, due to decreased evaporative cooling. A further complicating factor is the additional impact of changed abundance of host tree species on the community composition of epiphytic NVP. Thereby, host tree specificity not only depends on microclimate associated with a certain tree species but also on nonclimatic factors, such as bark structure and chemistry (Nascimbene *et al.*, 2020).

All habitat types

It is likely that NVP will show a dynamic response to warmer conditions and altered rainfall frequency and amount (Di Nuzzo *et al.*, 2021). However, the possible extent of this response is largely unknown, for several reasons: First, it is poorly known which factors determine the large observed differences between species of NVP in their potential for acclimation to warming (Colesie *et al.*, 2018). Observations from the Antarctic suggest that generalist species may be able to cope with substantially warmer conditions, while many specialist, often endemic, species may not (Sancho *et al.*, 2017, 2020). However, how habitat conditions drive this physiological specialization is unclear (Colesie *et al.*, 2014). Second, whether elevated atmospheric CO_2 concentration will have a relevant positive effect on the productivity of NVP is unclear (Coe *et al.*, 2012). Contrary to vascular plants, CO_2 limitation of NVP generally occurs under high water saturation, caused by reduced CO_2 diffusivity. As climate change will likely lead to more frequent dry conditions, when NVP are not CO_2-limited, the reduced active time may outweigh the potential benefits of CO_2 fertilization. At the forest floor, but also in peatlands and in certain tundra habitats, ambient CO_2 for NVP may be uncoupled from CO_2 concentration in the air (Tarnawski *et al.*, 1994), which represents additional uncertainty regarding the CO_2 response.

Research outlook

Our categorization scheme for habitat types of NVP (Fig. 2) shows that the organisms are able to survive under a large range of climatic conditions. Individual species, however, often seem to be specialized to a specific combination of microclimatic factors, including the pattern of climatic variability (see 'Open ground', 'Peatlands', 'Understory', and 'Vascular plants' in the Potential impacts of climate change on key ecosystem functions of NVP section). In general, the literature suggests that many species of NVP will be locally threatened if the characteristics of their habitats are substantially altered due to climate change (Table 1). Acclimation to seasonal variation of temperature is common, for instance (Lange & Green, 2005), but weather extremes may surpass the organisms' ability to acclimate (Maier *et al.*, 2018). While the climatic impact factors are largely consistent between different habitat types, the main ecosystem functions performed by NVP seem to be more habitat-specific. Thus, it is likely that the effects of climate change on NVP will affect a considerable range of different ecosystem functions around the world.

While the general direction of climate effects on NVP is relatively well constrained, quantitative estimates on their extent are highly uncertain. This is mainly due to knowledge gaps on several key overarching mechanisms, which determine the ability of the organisms for dynamic response: (1) acclimation to increased temperatures and altered hydrological conditions; (2) response to increased ambient CO_2; (3) role of (symbiotic) microbes; and (4) complex feedbacks between climatic factors, biophysical surface properties (e.g. albedo), and ecophysiological responses of NVP. While the relative importance of these poorly known response processes differs between habitat types, they all contribute substantially to the overall large uncertainty.

The dynamic response of NVP to climate change may occur not only at the individual level through phenotypic plasticity, but also at the population level through selection and adaptation to environmental change, and at the ecosystem level via shifts in community composition (Di Nuzzo *et al.*, 2021). To what extent ecosystem functions depend on the specific composition of nonvascular communities and how they will be affected by potential community turnover in the future is largely unclear.

To advance our understanding of NVP under changing climate, we suggest a threefold approach, which includes: (1) new or extended field and laboratory experiments and measurement techniques; (2) further development of modelling approaches; and (3) integration of models and data across scales.

Experiments and measurements

Current studies suggest a species-specific ability of NVP to acclimate to changed climatic conditions (Wagner *et al.*, 2014). Multispecies experiments that cover a large range of habitats and

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manipulate several climatic factors may thus provide essential insights into the mechanisms which enable certain species to acclimate more efficiently than others. The uncertain long-term response of NVP to elevated CO_2 may be addressed by multifactorial fertilization experiments, which include potential nutrient limitation of growth (Aerts *et al.*, 1992). This would be complemented by free-air CO_2 enrichment (FACE) experiments, which, until now, have seldom covered ecosystems dominated by NVP (Norby *et al.*, 2019).

Innovative measurement techniques will provide more detailed information on ecophysiological processes of NVP and their interactions with the environment, such as new sensors for determining biocrust wetness (Weber *et al.*, 2016), isotopic and automated gas exchange (Büdel *et al.*, 2018), and 3D analysis of surfaces of NVP (Caster *et al.*, 2021). Moreover, molecular approaches, such as metagenomics and metaproteomics, can help to characterize the (symbiotic) microbial community associated with NVP and understand their effects on NVP metabolism and functioning (Weston *et al.*, 2015; Torres-Benítez *et al.*, 2017; Maier *et al.*, 2018; Grimm *et al.*, 2021).

Further insights may be gained from (long-term) observation of relations between climate and nonvascular activity (and carbon balance) along spatial gradients through remote sensing that is calibrated to ground-based measurements (Rieser *et al.*, 2021). In addition, increasing the knowledge of species' spatial distributions, which is still poor, even for many large and common lichens (Stanton & Coe, 2021), may improve the recognition of the climatic ranges that nonvascular organisms are able to cope with and may also move forward taxonomy (Martellos *et al.*, 2014).

Modelling

Species distribution models (SDMs) have been used in recent decades to predict the occurrence of NVP, often based on bioclimatic envelopes (Giordani & Incerti, 2008), and assess the potential consequences of climate change on the abundance of nonvascular species (Nascimbene *et al.*, 2016). Extending this to trait-based approaches may allow for a more generalized way across taxa to assess not only how environmental factors shape traits of NVP, but also how traits of NVP affect ecosystem functions (Giordani *et al.*, 2014; Ellis *et al.*, 2021). Thereby, including the evolutionary history of species may help to constrain model predictions (Nelsen *et al.*, 2022). To advance the SDM approach further, it has been suggested to account for nonclimatic factors, such as habitat quality, and to include schemes for the representation of population processes, such as adaptation or migration (Ellis, 2019b).

Process-based dynamic vegetation models (DVMs) which focus on NVP are rare so far (Porada *et al.*, 2013; Launiainen *et al.*, 2015; Kim & Or, 2017). The main difference between the DVM and the SDM approach is that the transient response of organisms to (changing) climate is explicitly simulated in DVMs, so to assume an equilibrium with the environment is not required. Dynamic vegetation models are therefore often integrated in Earth System Models. Dynamic vegetation models of NVP compute physiological processes, such as photosynthesis or growth, in a mechanistic way, thereby considering either parts of the metabolism (N. Nikolić *et al.*, unpublished) or entire individuals (Porada *et al.*, 2013; Baldauf *et al.*, 2021). Simple nonvascular functional types have been included in several land surface models (e.g. Porada *et al.*, 2016; Park *et al.*, 2018; Druel *et al.*, 2019). Explicit simulation of physiological and morphological traits of NVP and their distributions in diverse nonvascular communities makes it possible to assess the role of community composition for ecosystem function, but is only considered by few models (Porada *et al.*, 2013). As for SDMs, a more detailed representation of population processes may improve DVM projections of climate change impacts on NVP. A key knowledge gap that may be addressed by process models is the role of complex feedbacks between NVP and climate, but this is complicated by uncertainty regarding the relevance of indirect effects of climate change on NVP, such as vascular plant dynamics or disturbance.

Model–data integration

While further developments of real-world experiments and modelling often take place rather independently from each other, we suggest that an integrated approach will substantially advance our understanding of the climate response of NVP. To allow for improved quantitative predictions on NVP-climate feedbacks, models need to account for the relevant functional traits regarding both the response of NVP to climate (change) and the effects of the organisms on climate (Ellis *et al.*, 2021). In addition, traits that are linked to other ecosystem functions will be affected by climate change, such as alteration of (soil) nutrient cycling or food webs (Cornelissen *et al.*, 2007; Concostrina-Zubiri *et al.*, 2021), and need to be included in modelling approaches, too. Thereby, the large observed variation in possible trait values (Mallen-Cooper & Eldridge, 2016) should be considered. While this use of functional traits is crucial for model advancement, the availability of observational data in this regard needs to be markedly improved. Global databases of plant traits, such as TRY (Kattge *et al.*, 2011), cover a relatively small fraction of the expected diversity in functional traits of NVP. Hence, a collective effort of the research community would enhance connections to already existing data and may lead to new insights on trait–environment relationships in NVP (Deane-Coe & Stanton, 2017; Mallen-Cooper *et al.*, 2020).

Furthermore, an improved understanding of physiological and ecological mechanisms of NVP is the key to enhancing the predictive power of models aiming at estimating the effects of NVP on biogeochemical processes. In particular, hypotheses on mechanisms behind acclimation and CO_2 fertilization, or the role of microbes, need to be implemented into models and then tested against observations from warming or CO_2 enrichment experiments. Thereby, it is crucial that physiological and ecological processes in models account for trade-offs between traits, because these may constrain the potential of NVP for dynamic response to changing climate. Increased photosynthetic capacity, for instance, results in increased maintenance respiration rate due to the required metabolic investment in enzyme pools and other structures (Bengtsson *et al.*, 2016; Wang *et al.*, 2017a). If the supply of water, light, and CO_2 is not sufficient to meet photosynthetic

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capacity, this may have an overall negative impact on the carbon balance of NVP (Wang *et al.*, 2017b).

Regarding potential shifts in nonvascular community composition, we suggest that the carbon balance of the organisms may serve as a good approximation for their relative ecological success, because (1) any photoautotroph needs to achieve positive net primary production (NPP) for survival in the long term; and (2) carbon from NPP may be invested in various physiological processes and biotic interactions, which determine intra and interspecific competitive strength. Furthermore, the carbon balance is applicable from the level of an individual organism to the ecosystem. Quantifying the effects of climatic factors on the carbon balance both through observations and modelling may thus enable prediction of the realized response of nonvascular communities under climate change. Thereby, it may not always be necessary to directly measure carbon fluxes in the field, but sufficiently long-term estimates of biomass and coverage from remote sensing (Smith *et al.*, 2015; Rodríguez-Caballero *et al.*, 2017; Erlandsson *et al.*, 2022) may also be used as a proxy for the accumulated carbon balance.

The broad scope and low resolution of our approach results in several limitations, which, however, may be addressed by future works. So far, we do not explicitly account for indirect or nonclimatic effects on NVP, such as human impacts, or consequences of climate change for other ecosystem components. Altered herbivory or disturbance frequency, for instance, may substantially modify various relations between NVP and ecosystem functions. This may be studied by modelling approaches, which include key ecosystem feedback mechanisms, but which still need to be developed.

Conclusion

According to our analysis, expected impacts of climate change on ecosystem functions and services of NVP will be negative in the majority of cases, meaning that the extent of associated functions will be reduced in many ecosystems. This includes protection of the soil structure against various environmental factors, nutrient input and carbon sequestration, and also climate regulation from the local to the global scale. The main climatic factors that affect NVP in this regard are increased ambient temperature (and, in some cases, decreased humidity), altered rainfall patterns, and more frequent weather extremes. Negative effects may mainly result from shorter active time, causing reduced net growth, and increased respiration costs, depending on the timing of increased temperature and changes in the pattern of hydration events. New research approaches will be required to quantitatively assess the extent of these impacts.

The potential loss of ecosystem functions implies that NVP should be included in the development of sustainable land management scenarios, thereby benefiting from research investment. Furthermore, research in the area of nature conservation should account for the functional role of NVP in ecosystems and may benefit from the addition of a stronger physiological perspective. Finally, consistent integration of NVP into Earth System Models may enable more accurate projections of future vegetation–climate feedbacks. To summarize, we highlight the avenues of new research, with a focus on functional traits and ecophysiological processes and trade-offs, to achieve an improved understanding of the future role of NVP in global ecosystem functioning.

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Competing interests

None declared.

Author contributions

PP developed the concept of the viewpoint and wrote the article in exchange and with input from MYB, MBB, CC, CJE, PG, UH, YM, SL, JN, IP, JRQ, ER-C, KR, LGS, CS, SS, JTVS, MV, BW and DJW.

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Data availability

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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