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South American mountain ecosystems and global change – a case study for integrating theory and field observations for land surface modelling and ecosystem management

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ABSTRACT

Background: Plot-based monitoring has yielded much information on the taxonomic diversity and carbon (C) storage in tropical lowland forests of the Amazon basin. This has resulted in an improved understanding of the relationship between lowland forest biomass dynamics and global change drivers, such as climate change and atmospheric CO₂ concentration. Much less attention has been paid to the mountain ecosystems of South America that comprise montane forests and alpine vegetation (páramo, puna, high Andean grasslands, wetlands, and alpine heath). This vegetation complex provides a variety of ecosystem services and forms a natural laboratory along various physiographic, geological and evolutionary history/biogeography, and land use history gradients.

Aims: Here, we review existing empirical understanding and model-based approaches to quantify the contribution of mountain ecosystems to ecosystem service provision in the rapidly changing socioecological setting of the South American mountains. The objective of this paper is to outline a broad road map for the implementation of mountain vegetation into dynamic global vegetation models (DGVM) for use in Earth System Models (ESM), based on our current understanding of their structure and function and of their responsiveness to global change drivers. We also identify treeline processes, critical in mountain ecosystems, as key missing elements in DGVMs/ESMs, and thus explore in addition a treeline model.

Methods: Stocktaking of the availability of empirical data was undertaken from eight research sites along the Andes and in south-eastern Brazil. Out of eight sites, two (one each in Venezuela and Brazil) had some climate, ecological and ecophysiological data potentially suitable to parametrise a DGVM. Tree biomass data were available for six sites. A preliminary assessment of the Joint UK Land Environment Simulator (JULES) DGVM was made to identify gaps in available data and their impacts on model parametrisation and calibration. Additionally, the potential climate-determined elevation of the treeline was modelled to check the DGVM for its ability to identify the transition between the montane forest and alpine vegetation.

Results: Outcomes of the evaluation of the JULES land surface model identified the following key processes in montane forests: temperature-related decrease in net primary production, respiration, and allocation to above-ground biomass and increase in soil C stocks with elevation. There was a variable agreement between simulated biomass and those derived from field measurements via allometric equations.

Conclusions: We identified major gaps between data availability and the needs for process-based modelling of South American mountain vegetation and its dynamics in DGVMs. To bridge this gap, we propose a transdisciplinary network, composed of members of the theoretical/modelling and empirical scientific communities, to study the natural dynamics of mountain ecosystems and their responses to global change drivers locally, regionally and at the continental scale, within a social-ecological system framework. The work presented here forms the basis for the design of data collection from field measurements and instrumental monitoring stations to parametrise and verify DGVMs. The network is designed to collaborate with and complement existing long-term research

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initiatives in the region and will adopt existing standard field protocols. Complementary protocols will ensure compatibility between field data collection and data needed for process-based and empirical models.

Introduction

The objective of this paper is to outline a broad road map for the implementation of mountain vegetation and critical processes (e.g. those associated with the treeline) into dynamic global vegetation models (DGVMs)/Earth System Models (ESMs), based on our current understanding of their structure and function and of their responsiveness to global change drivers. After providing a review of mountain vegetation and its underlying factors, focusing on South America, we first report the data availability at long-term mountain ecosystem research sites in South America and contrast it with data needed for parametrising and validating DGVMs. Second, we present preliminary output from the Joint UK Land Environment Simulator (JULES)-DGVM, contrasting the output with estimated biomass and NPP data in the field. Third, we briefly consider the specificities of mountain environments that are required to be taken into consideration by DGVM and ES modellers. Finally, we outline the proposed collaborative network of modellers and empirical scientists across South American mountain research sites to harmonise data and information collection, processing and interpretation, including interpretation for global, regional and local stakeholders in a focused effort to make ESMs accessible to those who produce the impacts by their land use decisions and who need to be empowered by evidence-based science to manage locally land use so as to minimise impacts globally.

Mountains and mountain ecosystems

Mountains worldwide cover 12.3% of the Earth's terrestrial surface (Körner et al. 2011), with

estimates diverging according to the definitions of 'mountain'. Rising from the lowlands, mountains maintain a tight hydrological connectivity (Williams et al. 2015) and form a characteristic biophysical continuum. Some elements of this continuum undergo predictable changes with elevation (atmospheric pressure, temperature, and the soil-vegetation complex; Nagy and Grabherr 2009; Körner 2021a); other features such as geomorphology or precipitation patterns follow less predictable patterns. The continuum of lowland – mountain ecosystems in non-water-limited conditions consists of various forest types replaced by low-stature herbaceous – shrub (alpine) vegetation on high mountains (see Humboldt and Bonpland (2010) for an early description from the Andes, originally published in French in 1807). Throughout this paper, the generic term mountain ecosystems encompasses montane forest and alpine vegetation (see Table 1 for definitions); montane is applied specifically to forest found between the lowland forest and the treeless alpine vegetation. In montane forests, the dominant thermophilus lowland tree families are substituted by a different suite of taxa, adapted to cooler climatic conditions with elevation, and, at the cold upper limit, forest is replaced by treeless alpine vegetation (Nagy and Grabherr 2009; Körner 2012, 2021a). These features are essential to understand the natural dynamics of mountain ecosystems and the potential human benefits that can be derived from them.

South American mountains

Mountain ecosystems provide essential ecosystem services (Locatelli et al. 2017) such as slope protection, soil retention, hydrological regulation (Hamilton and

Table 1. Definitions adopted for mountain vegetation (after Grabherr et al. 2003; Körner 2007; Nagy and Grabherr 2009).

| Feature/entity | Definition |
|--|--|
| Mountain vegetation | Montane forest and abutting low-stature alpine vegetation |
| Montane forest | The forest belt between lowland forest and alpine vegetation |
| Treeline (potential cold-limited treeline) | The line where closed groups of trees taller than 3 m ends |
| Treeline ecotone | The zone between the closed forest line (also called timberline) and tree species line, the line beyond which no individuals of tree species occur |
| Alpine | The zone between the treeline and the upper limit of vegetation (with closed patches of vegetation dominating the landscape) |
| Tropical alpine – central Andes | Puna: arid and semi-arid dwarf-shrub vegetation; high Andean grasslands, largely dominated by bunch grasses |
| Tropical alpine – northern Andes | Páramo: a diverse alpine ecosystem complex in the humid Andes, in many places with giant rosette plants |
| Nival/aeolian | The zone of open sparse vegetation above the upper edge of the alpine belt; permafrost present |

Bruijnzeel 1997), carbon (C) storage and sequestration (Spracklen and Righelato 2014; Duque et al. 2021) and biodiversity (Körner 2002). Tropical montane forests are important biodiversity centres (Hamilton 2002; Gradstein et al. 2008) with a variety of biogeographic origins and histories (Groot et al. 2011; Flantua et al. 2016), harbouring a large number of endemic organisms (Veblen et al. 2007); mountain ecosystems in the Andes and the south-eastern Brazilian mountain range host the highest plant diversity on Earth (Myers et al. 2000). Mountain ecosystems in Central and South America occur from northern subtropical (e.g. Mexico) via tropical evergreen wet (Costa Rica, Colombia, Venezuela) and tropical dry (central Andes) to southern temperate (Patagonia) latitudes (Veblen et al. 1996; Garreaud and Aceituno 2007); they include tropical montane cloud forests (World Conservation Monitoring Centre 1997; Mulligan 2010) that also occur in the south-eastern Brazilian mountain ranges, mostly in the Atlantic Forest biogeographical domain (de Barcellos Falkenberg and Voltolini 1995). Mountain ecosystems in South America have historically been under pressure from land conversion (Ellenberg 1979; Balée 1998; Gade 1999; Denevan 2001), increasingly so following recent population expansion (Hamilton et al. 1997; Kappelle and Brown 2001; Navarro and Maldonado 2002; Spehn et al. 2006), and from recent climatic changes (Pounds et al. 1999; Fadrique et al. 2018). Rates of warming in the Andes have been reported to be three times higher than elsewhere in South America (Vuille and Bradley 2000; Vuille et al. 2018), and a higher than global average warming of 5–6 K is predicted by the end of the twenty-first century (Urrutia and Vuille 2009); a temperature change comparable to that which followed the last glacial maximum in the current interglacial. Therefore, climate change together with land use change pose significant challenges to the diversity and functioning of mountain ecosystems in the future (Corlett 2012). In particular, the subtropical and tropical mountain ranges that are most affected by land use in South America form a high-priority area (see chapter 24 Mountain systems in Hassan et al. 2005) in which to study the likely responses of tropical mountain ecosystems under future environmental change.

Global change drivers and their representations in models

Global change drivers that affect biodiversity and ecosystem services include climate change, land

use and land cover change, atmospheric nitrogen (N) deposition, elevated CO₂ concentration and biotic interaction between native and non-native biota. The most impactful of these in most of South America are land use change and climate change (Tovar et al. 2011), followed by invasive species. To plan and undertake the management of ecosystems to maintain their services in a sustainable manner, adequate conceptualisation, and tools such as models and decision support tools are required. Such tools have been developed for local and regional implementation (Kareiva et al. 2012). However, to aggregate the local and regional impacts of the use of ecosystem services at the global scale, DGVMs, which combine physico-chemical and biological processes (see e.g. Kruijt et al. 2016 for a review of their application in the Amazon basin), have been used to link biosphere (soil-vegetation) atmosphere as the land components of ESMs. DGVMs have failed in the past to capture the functional changes necessary to simulate the responses of tropical forest to warming and water deficit, which drive altered functionality and changes in tree demographical processes such as mortality, according to size and functional type (Galbraith et al. 2010). Since then, progress has included adding new functionality in terms of plant drought response (Eller et al. 2020), new trait datasets to improve the definition of vegetation characteristics and differentiate plant functional types (Harper et al. 2016) and development towards explicit ecosystem demography (Argles et al. 2020).

Dynamic Global Vegetation Models (DGVMs)

First-generation DGVMs (e.g. Sitch et al. 2003) have adopted simple schemes to allocate net primary production (NPP) to plant growth, and some models have included explicit simple representation of vegetation dynamics and disturbance. A new generation of DGVMs includes more biological processes, e.g. nutrient cycling (N and phosphorous, P; Nakhavali et al. (2022)), use new empirical data, e.g. trait information, to better define vegetation in terms of plant functional traits (PFTs; Fyllas et al. 2017), or are individual-based (e.g. Scheiter and Higgins 2009), and contain a more comprehensive representation of vegetation demography (Smith et al. 2001; Argles et al. 2020) with explicit accounting for mortality, plant succession and temporal development of age/size classes, and explicit

disturbance (e.g. fire-enabled DGVMs; Rabin et al. 2017). DGVMs lack representation of plant migration (but see Lehsten et al. 2019 for some recent advances) and are unable to mechanistically simulate the treeline, both of which are highly important for understanding vegetation dynamics in mountain ecosystems. For treeline, DGVMs either adopt a simple climate envelope approach, e.g. based on growing degree day limits (e.g. Sitch et al. 2003), or rely on primary productivity variation across functional groups to define ecotones (e.g. JULES). There is thus an urgent need to incorporate new mechanistic understanding on treeline dynamics into ESMs. This is also timely as DGVMs are developing to include non-structural carbohydrate pools (e.g. Jones et al. 2020) and thus be able to better differentiate photosynthesis from growth processes, which are critical for treeline prediction.

DGVMs in mountain environments

To date, little attention has been paid to tropical montane forests and other mountain ecosystems by the DGVM and ESM communities (e.g. Clark et al. 2011) and the current generation of DGVMs does not include an adequate representation of the functioning of mountain ecosystems, e.g. treeline dynamics. In part, this is due to the coarse resolution of models, e.g. DGVMs typically run at 0.5 degrees (50 km at the equator) and ESMs at coarser resolution (only now at ca. 100-km resolution). The first generation of ESMs in the 2000s ran at ca. 300–400 km resolution and thus would average large elevation gradients in mountain regions. As computational power has improved, DGVMs are only now able to run over more realistic elevation gradients, making this work timely. In addition to the scale issue, adequate representation of the functioning of mountain ecosystems, e.g. treeline dynamics, can be overcome by adequate inclusion of current empirical understanding into models, one important issue being the representation of growth limitation by factors other than the availability of photosynthates, which itself has been shown to not limit the growth of trees at the treeline (Körner 2021b). Accurate ESM representation of tropical mountain ecosystems regarding climate C feedbacks (e.g. Zeng et al. 2021) will substantially strengthen the ability to formulate well-targeted regional climate change policies and climate adaptation strategies, and therefore to build resilience in tropical mountain environments.

The output from DGVM models, and thus their information quality, depends on the one hand, on the formulation of the model components and the data that the model uses, and, on the other, on the spatial scale of the projection. The local and regional implementation of DGVMs is not without problems (see e.g. Bachelet et al. 2015) and the coarse spatial resolution of input data in environmentally heterogeneous mountain terrain is expected to have a major impact on the performance/reliability of models. This is partly because of the changes associated with the area and elevation range represented by raster grid cells in mountains in grid-based implementation (see e.g. Spracklen and Righelato 2014). The first generation of ESMs in the early 2000s, for example, ran with grid cells of 250 km × 375 km resolution at the equator (Cox et al. 2000). In flatlands, there is no vertical component involved, i.e. climate variables can be assumed to be homogeneous in a grid pixel. In contrast, in steep mountain terrain a vertically projected pixel equal in size to that in flatlands has a larger surface area, can span several hundred metres in elevation and thus can contain heterogeneous environmental information. More importantly, DGVMs represent broad generic vegetation types formulated based on lowland types, and they lack a mechanistic representation of montane vegetation and especially that of potential cold-limited treelines (cf. Paulsen and Körner 2014 for an empirical model of treelines, based on climate). To include this mechanistic basis, one would be required to account for the differences between the limitation of photosynthesis and growth (Körner 2015), knowing that the demand for photosynthates for growth is defined by the sink capacity of plants, which diminishes more with temperature limitation along elevation in mountain ecosystems than their photosynthetic capacity.

The Joint UK Land Environment Simulator (JULES)

Some of the studies that have applied DGVMs to montane forest include JULES (Best et al. 2011, Clark et al. 2011), the land surface component of the UK ESM (UK Met Office Unified Model). JULES has been applied by Marthews et al. (2012) to the Amazon – Andes elevation transect (3.3 km) in Peru, part of the Global Ecosystem Monitoring (GEM) network, but it failed to adequately

represent NPP in the upper montane forest. A follow-up modelling study by Fyllas et al. (2017), not using JULES, has successfully represented the empirically observed decline in NPP with elevation (proxy for temperature), using the Traits-based Forest Simulator (TFS), relating solar radiation to plant functional types (leaf dry mass per area, leaf N and P concentrations, and wood density) along the same transect. The authors have suggested that the correlation of trait variation with temperature might be enough to capture temperature effects, even without considering the possible difference in temperature sensitivity of photosynthetic parameters (e.g. Feeley et al. 2020) in vegetation across this large temperature gradient. It remains to be elucidated whether the optimum temperature for photosynthesis (and tissue growth) and photosynthetic parameters differ across vegetation with elevation in South American mountains and whether this information is needed to incorporate realism into DGVMs when simulating montane forest vegetation and mountain ecosystems in general.

Mountain terrain constitutes a high-energy environment and thus mountain ecosystems are particularly sensitive to the conversion of forest to pasture or agricultural use, which may result in degradation and complete removal of vegetation cover (Körner 2002). Thus, projecting with reasonable precision the impacts of land use and land cover change on ecosystem services and biodiversity is imperative (Peters et al. 2019). Recent work by Zeng et al. (2021) has attempted to quantify the impacts of local deforestation in four of the world's tropical mountain ranges, including the Espinhaço Range, Brazil, a ca. 1200-km-long mountain chain, largely in a dry inland tropical climate. Their work was based on the tenet that conversion of forest land to crops affects climate by causing a decrease in surface roughness and evapotranspiration, which in turn leads to warming, not compensated by the cooling effect of a coincidental increase in albedo (albedo effect is only applicable to the nival belt in tropical mountains, most of which lack extended periods of snow cover). While an important contribution, Zeng et al. (2021) did not consider the central and northern Andes or the south-eastern Brazilian ranges where tropical montane rain forests predominate and where population pressure is greatest. Thus, although Zeng et al. (2021) point in the right direction, their work fails to fully address a major weakness in DGVM/ESM in adequately projecting land cover and land use change impacts

in mountains on atmospheric composition and processes. This paper introduces an initiative that encompasses the Andes and other major South American mountains (Figure 1).

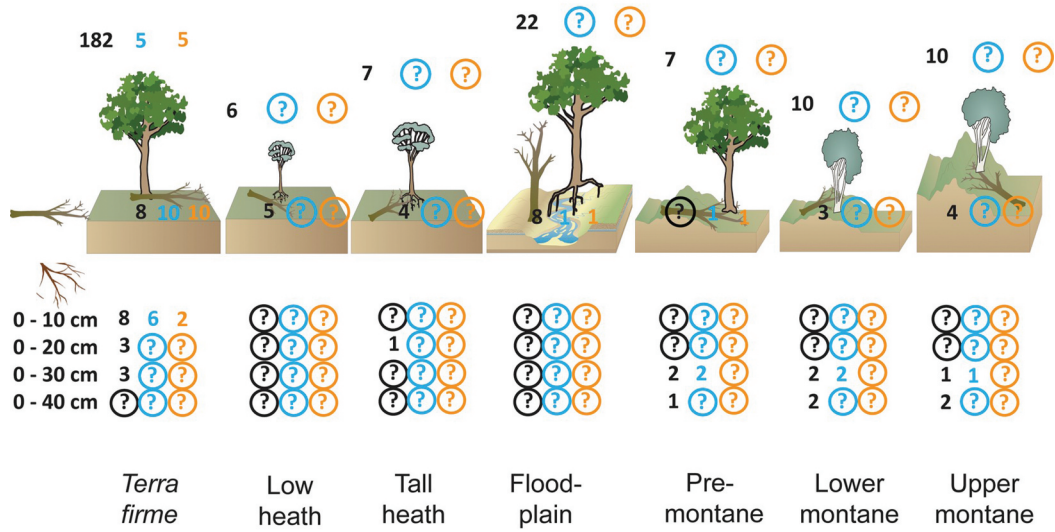
Field data for parametrising and validating models in South America

To be able to make reliable predictions, models require reliable environmental and biological (biophysical) data and plausible land cover and land use change scenarios. The empirical work on data collection and analysis (e.g. measurement of trees in permanent sample plots and statistical models to relate biomass change to available environmental data) in South America commenced in an organised way 20 years ago, partly building on earlier initiatives (Malhi et al. 2002). The Amazon Forest Inventory Network (RAINFOR; <http://www.rainfor.org/en>) was established to record and interpret ecological and biogeochemical changes across the Amazon basin over precipitation and temperature gradients and in response to their temporal changes (ForestPlots.net et al. 2021). The objectives included relating forest dynamics, i.e. growth and mortality, to spatio-temporal variation in environmental drivers, e.g. dry season length, soil nutrients, to increasing atmospheric CO₂ concentrations, and forest fragmentation owing to deforestation (Malhi et al. 2002), the latter principally occurring at the southern and northern edges of the Amazon rain forest where it meets the savanna. The RAINFOR network has grown dynamically and has made a significant contribution to our understanding of old-growth (but see McMichael (2021) on the ecological legacies of past human activities) lowland rain forest dynamics in the Amazon basin (Phillips et al. 2009; Quesada et al. 2012). Subsequently, the network expanded, and after 20 years, it encompasses a worldwide network (Qie et al. 2017; ForestPlots.net et al. 2021) that today allows to make complex analyses of forest biomass patterns, and relate them to multiple causes such as climate (past and present) and biogeography (Sullivan et al. 2020). The RAINFOR network and its current extended version, ForestPlots.net (ForestPlots.net et al. 2021), have served as a solid empirical witness of evidence-based science using its extensive network of on-the-ground local experts. It has also been providing useful information for ground-truthing



Figure 1. Broad vegetation types of the main mountain areas of South America. Andean montane forest areas (northern Andean montane forests) central Andean yungas and Bolivian dry forests; and the temperate Valdivian and sub-polar Magellanean forest in the south are in dark green; tropical alpine areas (páramo, puna) in brown; the high-elevation parts of the southern Andean Mediterranean scrub are in ochre (after Olson et al. 2001). Outside of the Andes, forest areas are indicated in the Talamanca range, the Tepuis highlands, the south-eastern Brazilian mountain range, along with the dry forests of the Espinhaço Range and its saxicolous grasslands. The numbers indicate the network of mountain research sites that took part in the assessment of their suitability for participating in the formation of a long-term interdisciplinary research network, formed by empirical scientists and modellers to better represent mountain environments in Earth System modelling; 1, Venezuelan Andes; 2, Colombian Andes; 3, western Ecuadorian Andes; 4, Amazon - Andes transect, Peru; 5, Tucuman, north-western Argentina; 6, Cape Horn, Chile; 7, Serra da Mantiqueira, south-eastern Brazil; 8, Serra do Cipó, Espinhaço Range, Brazil.

POOLS C N P



PS: coarse roots calculated on ABG biomass; no figures for soil

Figure 2. Data availability (number of published studies) for carbon (black), nitrogen (blue), and phosphorus (orange) pools in above- and below-ground biomass and litter in lowland evergreen forest types and for montane forests on the Atlantic macroslope of the Andes in the Amazon basin. Information is based on an exhaustive literature search up to 2015 (Buscardo et al. 2016).

INPUTS and OUTPUTS C N P

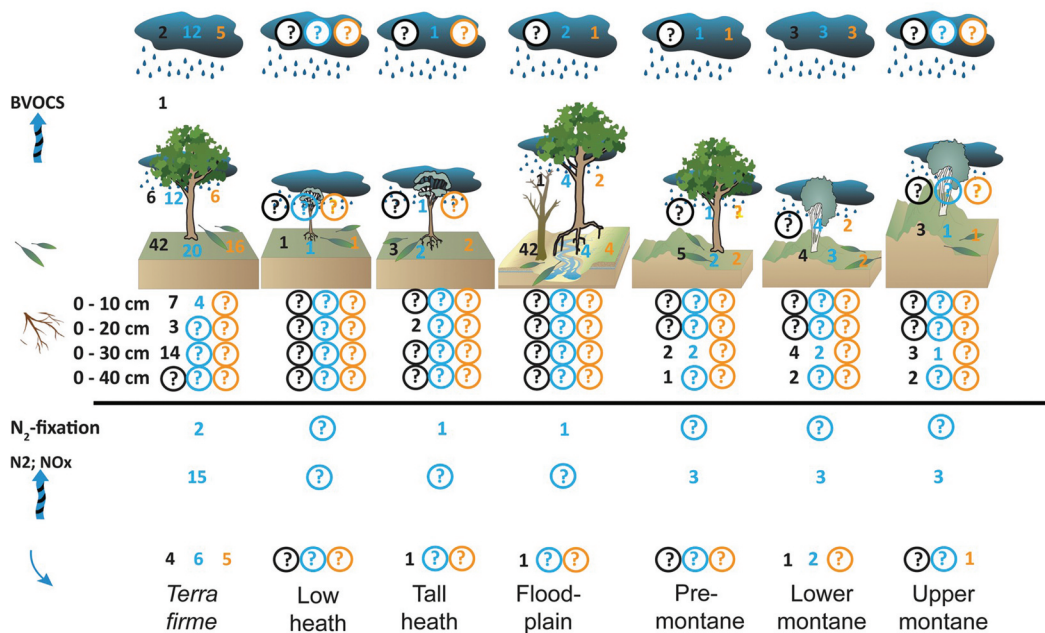


Figure 3. Data availability (number of published studies) for carbon (black), nitrogen (blue), and phosphorus (orange) fluxes in lowland evergreen and montane forests on the Atlantic macroslope of the Andes in the Amazon basin. Information is based on an exhaustive literature search up to 2015 (Buscardo et al. 2016).

of remote-sensing based approaches, not always without contradiction between ground and space-based approaches (Mitchard et al. 2014; Saatchi et al. 2014).

The various efforts to study South American montane forests have included the Amazon-Andes transect of the GEM network (Marthews et al. 2012) with six sites in Peru (Malhi et al. 2021) from tropical lowland to upper montane forest (e.g. Girardin et al. 2014; see additional site-specific results in *Plant Ecology & Diversity*, Volume 7, Issue 1–2 (2014)). The Andean Forest Network (<https://redbosques.condesan.org/>) of the tropical and subtropical Andes, part of ForestPlots.net has begun to contribute with knowledge on forest dynamics and biometric data (Malizia et al. 2020). The authors have reported an increase in stem (≥ 10 cm diameter at breast height (DBH)) density and basal area with elevation (a somewhat unexpected result from a physiographic point of view that is probably due to most of the study plots being in secondary forests) and a decrease in species richness; away from the equator, there is an apparent decrease in both stem density and species richness. Duque et al. (2021) have analysed a subset of the same dataset by relating biomass change to climate and phylogenetic community composition and found that, overall, the stem (≥ 10 cm DBH) biomass in the reported forest plots increased annually by about 1.2 Mg ha^{-1} in the last 20 years. In a subset of these plots in Ecuador, Llerena-Zambrano et al. (2021) have correlated leaf trait values with elevation, used as a proxy for temperature, and found that both succulence and sclerophylly became increasingly prominent with elevation in these forests.

Detailed ecological and ecophysiological studies complement biometry in very few locations outside of the Amazon-Andes transect, such as in the Mérida Andes, Venezuela (Delaney et al. 2009; Schwarzkopf et al. 2011; Quevedo-Rojas et al. 2018) and in the Serra da Mantiqueira, Brazil (Eller et al. 2020). However, results are not comparable as not all these initiatives have measured identical variables, and not all variables that are necessary or desirable to have for parametrising DGVMs are available. For example, an exhaustive literature review by Buscardo et al. (2016) identified large data and information gaps on C, N and P pools (Figure 2) and fluxes (Figure 3) in the montane forests along the Atlantic macroslope of the Andes and in lowland evergreen rainforest types in the Amazon basin.

As with vegetation above the treeline, a recent series of papers published in a special issue in *Plant*

Ecology & Diversity synthesised previous and ongoing work on the ecology, ecophysiology, adaptation and distribution of species at the treeline ecotone and in the páramo in the Mérida Andes, Venezuela (Arzac et al. 2019; Ely et al. 2019; Llambí and Rada 2019; Mavárez et al. 2019; Rada et al. 2019; Rodríguez-Morales et al. 2019; Sandoval et al. 2019). These articles, along with the collection of accumulated literature from this long-term interdisciplinary high mountain research site, provide a rich, yet incomplete data set for use in modelling.

Knowledge gaps

There are three facets of the empirical approach by ForestPlots.net that have left lacunae that call for the establishment of a complementary initiative, which we outline in this paper: (1) ForestPlot.net has overwhelmingly focused on lowland, old-growth rain forests, for their perceived overriding importance for the terrestrial C balance, at the expense of montane forests and other mountain ecosystems; (2) there has not been an explicit framework established to foster a scientific agenda-driven collaboration between modellers and empirical vegetation scientists/vegetation ecologists; and (3) most importantly, the forest plot based monitoring network needs to be expanded to include all land cover and land use types (owing to the prevalence of human impact on South American tropical mountain ecosystems, highlighted by Ellenberg (1979)), so that land use and land cover change and its relationship with climate change can be adequately modelled and DGVM/ESM model projections can be validated. Additionally, there is a dearth of targeted information on ecophysiology, except for the Amazon-Andes transect of GEM and data from a site in Venezuela and in Brazil. Such data are essential for parametrising DGVMs. Finally, the plot-based data collection, mostly for above-ground biomass, requires to be complemented by long-term flux measurements at master sites and by studies on soil biogeochemistry.

Data availability in South American mountains and a preliminary analysis using JULES

Materials and methods

Research sites

The eight sites in this study (Figure 1) encompass diverse climate, land use history and biogeography (Table 2). The Andean latitudinal transect includes Sites 1–5, which are all part of the Andean Forest Network. A detailed country

Table 2. Characteristics of the sites proposed for inclusion in a long-term social ecological research network in South American mountains to integrate empirical and modelling studies for an adequate representation of mountain environments in dynamic vegetation and Earth System modelling. See Figure 1 for the location of the sites.

| Site | Region | Climate | Vegetation | Ecosystem service (ES) | Stakeholders – ES use |
|-------------------------------|--------------------------------|------------------------------------|---|---|--|
| 1 – Mérida Andes, Ve | Venezuelan Andes | Humid tropical | Alpine (páramo), montane forest | Provisioning (agriculture, livestock husbandry and water supply); cultural (scientific research) | Municipality, smallholders, scientists and NGOs |
| 2 – Cordillera Central, Co | Colombian Andes | Humid tropical | Wet montane forest | Provisioning (water: hydroelectricity production, drinking and irrigation); regulating (carbon storage and sequestration); cultural (conservation of biodiversity and scientific research) | Municipality, smallholders, indigenous communities, scientists and NGOs |
| 3 – Pichincha, Ec | Western Ecuadorian Andes | Humid tropical, alpine, montane | Alpine (páramo), montane forest | Provisioning (water supply); regulating (carbon storage and sequestration); cultural (conservation of biodiversity and scientific research) | Municipality, smallholders, conservation authorities, water authority and NGOs |
| 4 – Amazon-Andes transect, Pe | Madre de Dios – Cusco | Seasonal tropical, montane, alpine | Alpine (puna), montane forest | Provisioning (livestock husbandry, agriculture and water); regulating (carbon sequestration); cultural (scientific research and conservation of biodiversity) | Municipality, indigenous community and scientists |
| 5 – Tucuman, Ar | North-west Argentina | Subtropical, montane, alpine | Alpine (puna), pre-puna, montane forest | Provisioning (livestock husbandry and water); regulating (carbon sequestration); cultural (scientific research and conservation of biodiversity) | Municipality, smallholders, herders and scientists |
| 6 – Omora Park, Cl | Cabo de Hornos | Temperate, subantarctic | Alpine heath; <i>Nothofagus</i> forest | Provisioning (water supply); regulating (carbon sequestration); cultural (recreation, research and conservation of biodiversity) | Municipality, indigenous Yahgan community, navy, tourism industry and scientists |
| 7 – PEC-LTER, Br | Serra da Mantiqueira | Tropical, (lower) montane | Mixed <i>Araucaria</i> – broadleaf montane forest, open shrubby grassland | Provisioning (water); supporting (biogeochemical cycles); regulating (carbon sequestration); cultural (recreation, scientific research and conservation of biodiversity) | Municipality, tourism industry, property speculators; local community, conservation authorities and scientists |
| 8 – SC-LTER, Br | Serra do Cipó, Espinhaço Range | Tropical, lower montane | Open grassy – shrubby vegetation (<i>campo rupestre</i>); scattered patches of various forest types (moist deciduous, seasonally dry, gallery); Cerrado | Provisioning (water: hydroelectricity production, domestic consumption and irrigation; medicinal plants; fodder); supporting (biogeochemical cycles); regulating (below-ground carbon storage); cultural (recreation, scientific research and conservation of biodiversity) | Municipality, tourism industry, agribusiness, property speculators; local community, conservation authorities and scientists |

account of the subtropical and tropical Andean montane forests is available in Kappelle and Brown (2001). Site 1, Mérida Andes, Venezuela has tropical moist broadleaf montane and cloud forest with abutting páramo (see definitions of alpine vegetation types in Nagy and Grabherr 2009); the site has a history of over 50 years of ecological research (Llambí and Rada 2019). Site 2, Colombian Andes, consists of a set of permanent plots of old growth forest, with elevations ranging from 1000 to 3400 m a.s.l. with major vegetation types corresponding to wet montane forest (Alvarez et al. 2012; Álvarez-Dávila et al. 2017). Site 3, Western Ecuadorian Andes, Ecuador, consists of a set of forest plots along 3000 m of elevation (Llerena-Zambrano et al. 2021), with abutting páramo that contains a long-term research site in the Yanacocha Reserve (Duchicela et al. 2021). Site 4, Peruvian Andes, includes tropical montane forest along an elevation gradient in the Peruvian part of the Amazon basin (Girardin et al. 2014) and abutting puna above the treeline. Site 5, in Tucuman, Jujuy and Salta provinces, Argentina, has a set of forest plots that have been studied (dynamics, structure and composition) since the early 1990s (Malizia et al. 2020). These plots are part of the Subtropical Permanent Plot Network (RedSPP, <https://ier.conicet.gov.ar/red-subtropical-de-parcelas-permanentes-redspp/>) that provides data of long-term plot monitoring of subtropical montane forests of Argentina. Site 6, Omora Park, southern Chile, represents an old-growth temperate southern beach (*Nothofagus* spp.) montane forest ecosystem, close to the most southerly occurrence of trees, in a varied landscape (elevation from sea level to treeline at ca. 600 m a.s.l.), with abutting alpine vegetation (Rozzi et al. 2007). There are two additional sites (7 and 8) in south-eastern Brazil. Site 7, Campos do Jordão, represents a Long-term Socio-Ecological Research (LTSER) site, in the Mantiqueira Range <https://deims.lter.peld-pecj.ib.unicamp.br/>. It has a mosaic of mixed conifer – broadleaf evergreen montane rain forest with *Araucaria angustifolia* and open shrubby grassland vegetation (Robim and Pfeifer 1988). Data from the ‘Cloud Forest Sensing Project of Microsoft’ project site, adjacent to the LTSER site, have ecohydrological data for sap flux, soil moisture content and climate variables for the period between 2015 and 2017 and additional information on floristic composition and on some plant functional traits (xylem and leaf hydraulics, leaf gas exchange, wood density) are also available (Eller et al. 2018; Bittencourt et al. 2019).

Site 8, Serra do Cipó LTER site in the south of the Espinhaço Range, represents patchy low-stature montane forest (Coelho et al. 2018) embedded in an area dominated by open vegetation (‘rupestrian grassland’ (Coelho et al. 2016)) where the *Cerrado* or Brazilian savanna meets the Atlantic rain forest, thus representing the dry end of the Atlantic montane forest spectrum.

Data inventory and analysis

A workshop was held with representatives from all the above sites in Campinas, Brazil, 2019, to make an enumeration of data availability collected within existing ecological research programmes. The data and information for energy and water flux measurements were collected and catalogued according to data requirements specified for the JULES model (tables 1–2 in Best et al. 2011); and for ecophysiological data (Clark et al. 2011) to assess the availability of data required to drive process-based models. These included atmospheric (radiation, temperature, precipitation and barometric pressure), soil (thermal and hydric properties) at hourly time scales and ecophysiological (leaf structural and photosynthetic traits) variables. Additionally, the availability of biomass data and measured/estimated prognostic variables (land surface, canopy, and soil) were catalogued.

The information was semi-quantitatively scored for each site (Table S1) on a scale of 0 (no data) to 1 (complete data), at intervals of 0.1, and displayed in a rose diagram to inform the level of completeness of data availability and to identify data gaps.

JULES-DGVM modelling with available information

The C balance and biomass of tropical montane forests were modelled at six sites that had permanent plot data with biomass estimates, i.e. five sites in the Andes and one from south-eastern Brazil (for data availability see Table S1). The objective was to compare model projections across the sites using parameters for lowland evergreen broadleaved tropical trees (EBTtr; Harper et al. 2016) versus a modified more montane forest-specific parametrisation. The initial model parametrisation was made following Harper et al. (2016) for EBTtr, except for leaf N content per leaf area (N_a) and leaf mass per area (LMA), whose values were taken from the study by Bahar et al. (2017) for lowland tropical forest trees. In the JULES implementation used, the ratio of foliar N_a to LMA controls the maximum carboxylation rate of Rubisco at 25°C (V_{cmax25}),

through a linear regression (Harper et al. 2016). We set the empirical coefficients of the $V_{\text{cmax}25}$ and N_m (N_m , leaf N content on a mass basis) relationship so that the N and LMA values would reproduce the values reported by Bahar et al. (2017) for $V_{\text{cmax}25}$ at $35.9 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Subsequently, the parameters for lowland EBTtr were gradually changed to match values observed at montane forest sites. At first, a set of simulations were conducted where the LMA values were altered to match those for montane species reported by Bahar et al. (2017), while maintaining $V_{\text{cmax}25}$ constant by adjusting the regression coefficients. Then, in addition to LMA, the values of N_a and the empirical coefficients of the $V_{\text{cmax}25}$ vs. N_m regression were altered to produce the $V_{\text{cmax}25}$ values reported by Bahar et al. (2017) for montane forest species ($48.8 \mu\text{mol m}^{-2} \text{s}^{-1}$). Finally, the values of the parameters that give the $V_{\text{cmax}25}$ response to temperature in JULES, T_{upp} and T_{low} were changed (Clark et al. 2011). We set T_{upp} and T_{low} to 40°C and 10°C , respectively, following Vårhammar et al. (2015) for African montane tree species.

The values of T_{upp} and T_{low} used in JULES were calibrated to match the optimal temperature for Rubisco activity reported for montane species by Vårhammar et al. (2015). For a description of the parameter values and references for each set of simulations, see Table S2.

The model was initialised by spinning it up for ca. 500 years by recycling its driving data. Additional information used to initialise the model soil C pools was taken from Delaney et al. (2009). The Climatic Research Unit Time series (CRU TS4.0) of meteorological data for 1901–2015, gridded to a resolution of $0.5 \text{ deg.} \times 0.5 \text{ deg.}$, was used to drive the model. The model was run, without competition among plant functional types, for a single grid cell fully covered by EBTtr (Cox 2001) in JULES v.4.6.

Modelling of the potential climatic treeline – TREELIM

The model was implemented to engage and inform both the DGVM and empirical community.

The elevation of the potential climatic treeline was modelled using the TREELIM model, following Paulsen and Körner (2014), in 19

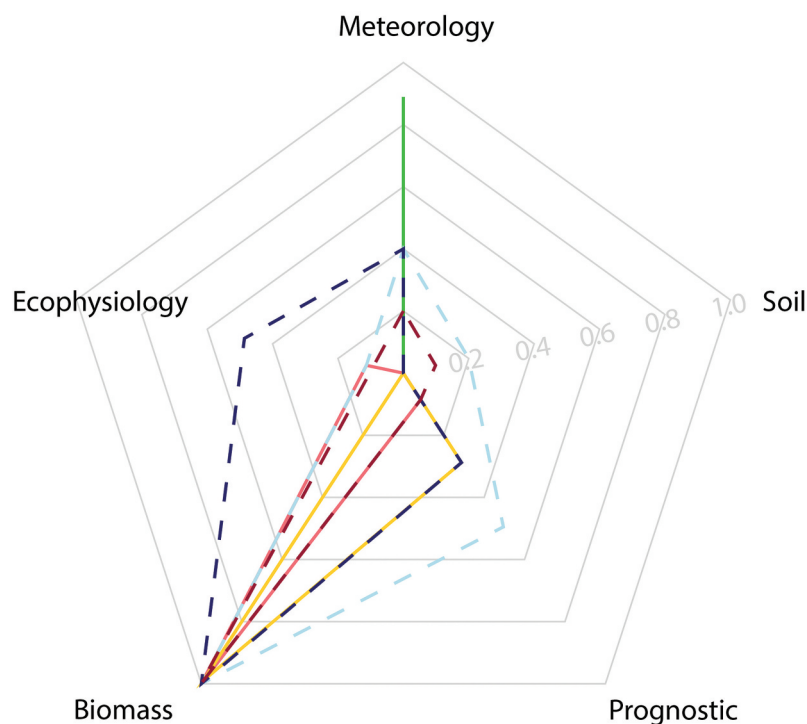


Figure 4. The classification of research sites based on their data availability for process-based modelling to contribute to Earth System modelling in the Andes and in the south-eastern Brazilian mountain ranges. The list of variables was compiled from Best et al. (2011) and Clark et al. (2011) and each variable per site was scored on a scale 0–1 (0, no data; 1, data available). Scores represent the proportion of data that for each of the four groups of variables (meteorology, soil, ecophysiology, and prognostic) plus biomass were available. Solid lines: green, Chile; ochre, Peru; salmon, Ecuador; Dashed lines: light blue Campos do Jordão, Brazil; dark blue, Venezuela; deep red, Argentina; Colombia has biomass and ecophysiology data which are masked by the ochre line of Peru and the salmon line of Ecuador; the Serra do Cipó, Brazil site has some meteorology data which are masked by other sites.

locations along the Andes and in two locations in south-eastern Brazil. The model combines thermal constraints, snow lie and hydrological constraints to determine the growing season length, whose duration (a minimum of 94 days per year) is used to delimit the elevation and latitude distribution of the tree life form. After implementing the model, local experts from the eight sites in this study were asked to verify the model output and report the actual treeline elevation observed locally.

Results

Data inventory and analysis

The data inventory (Figure 4) showed that some incomplete prognostic data (median score 0.3) were available at each site. Above-ground biomass data were the next most widely collected (seven out of eight sites, Figure 5). Additional information/data were scarce. Some atmospheric and plant eco-physiological data were available from three sites, and some soil-related information was available for a single site; for all these types of information the median score across all sites was 0. On a site basis, the Serra da Mantiqueira montane forest site had the most pieces of information (Figure 4), followed by the Venezuelan site. The rest of the sites, in addition to biomass, had little additional data; three sites reported some meteorological data (Omora Park, Chile being nearly complete at a score of 0.9).

Preliminary modelling JULES-DGVM

We found that JULES could simulate a realistic decline in forest productivity with elevation (Figure 6). The elevation responses were largely insensitive to the model parametrisation and could be produced with parameters typical of tropical lowland broadleaved rainforest vegetation. The model using lowland forest parameters predicted an NPP of $1.64 \text{ kg C m}^{-2} \text{ year}^{-1}$ at the reference lowland rain forest site, while the model using montane forest-specific parameters predicted a slightly higher NPP of $1.8 \text{ kg C m}^{-2} \text{ year}^{-1}$, which declined to $0.5 \text{ kg C m}^{-2} \text{ year}^{-1}$ at the uppermost site in Peru, regardless of parametrisation (Figure 6b). The slightly higher NPP produced by the montane forest parameters than by the lowland forest parameters at the lowland site was related to increased gross

primary production (GPP; Figure 6a), associated with the larger $V_{\text{cmax}25}$ values in montane vegetation. The increased GPP was partially offset by greater respiration rates (Figure 6c) minimising the change in NPP. The change in $T_{\text{upp}} / T_{\text{low}}$ made negligible difference to the simulation results compared with the simulation where only $V_{\text{cmax}25}$ was changed (Figure 6).

In addition to a decrease in NPP, plant respiration and allocation to above-ground biomass were also reduced with increasing elevation, while soil C stocks generally increased, except at the Argentinean site (Figure 6g). The montane forest-specific leaf and photosynthetic parameters decreased the simulated C use efficiency (CUE) by about 0.05 at the three coldest sites (Figure 6c). A montane-specific parametrisation also resulted in greater soil C content and drought stress, represented by a β -factor (Cox et al. 1998) that estimates how much photosynthesis has declined from its maximum value (i.e. $\beta = 1$) due to soil moisture stress at the colder higher elevation montane sites (Figures 6g–h).

Modelling of the potential climatic treeline – TREELIM

The elevation of the potential treeline modelled using TREELIM in the humid tropical Andes of Venezuela, and Ecuador was somewhat lower at between ca. 3800 m and 4000 m a.s.l. (Table S3) than at sites in Peru and Argentina at over 4000 m (with one exception). The corresponding values in south-eastern Brazil were lower than those in the Andes, estimated at between 3000 and 3400 m a.s.l. South of the Tropic of Capricorn, modelled treeline elevations ranged from 3400 m to 4000 m a.s.l. in Argentina.

Discussion

We identified acute shortages in local data availability for parameterising DGVMs, potential shortfalls in representing ecosystem processes specific to mountain environments in the model, and problems with using gridded implementation of the model in steep mountain terrain, without taking into consideration the required geometric correction. All these issues are discussed in more detail below.

Data availability

Our data inventory identified an acute shortage of local data (Figure 4, Table S1) that are required for

parameterising and calibrating JULES (Best et al. 2011; Clark et al. 2011) and other process-based models (e.g. White et al. 2000; Golinkoff 2010; Bachelet and Turner 2015; Hidy et al. 2021) for local implementation. These shortfalls concern, in the first place, field data on measured

ecophysiological variables that would allow adequate parametrisation of process-based DGVMs. It is important to reiterate the importance of local data in view of the complex biogeographical history of South America (Crisci et al. 1991; Veblen et al. 2007; Fiaschi and Pirani 2009; Fiaschi et al. 2016) and its

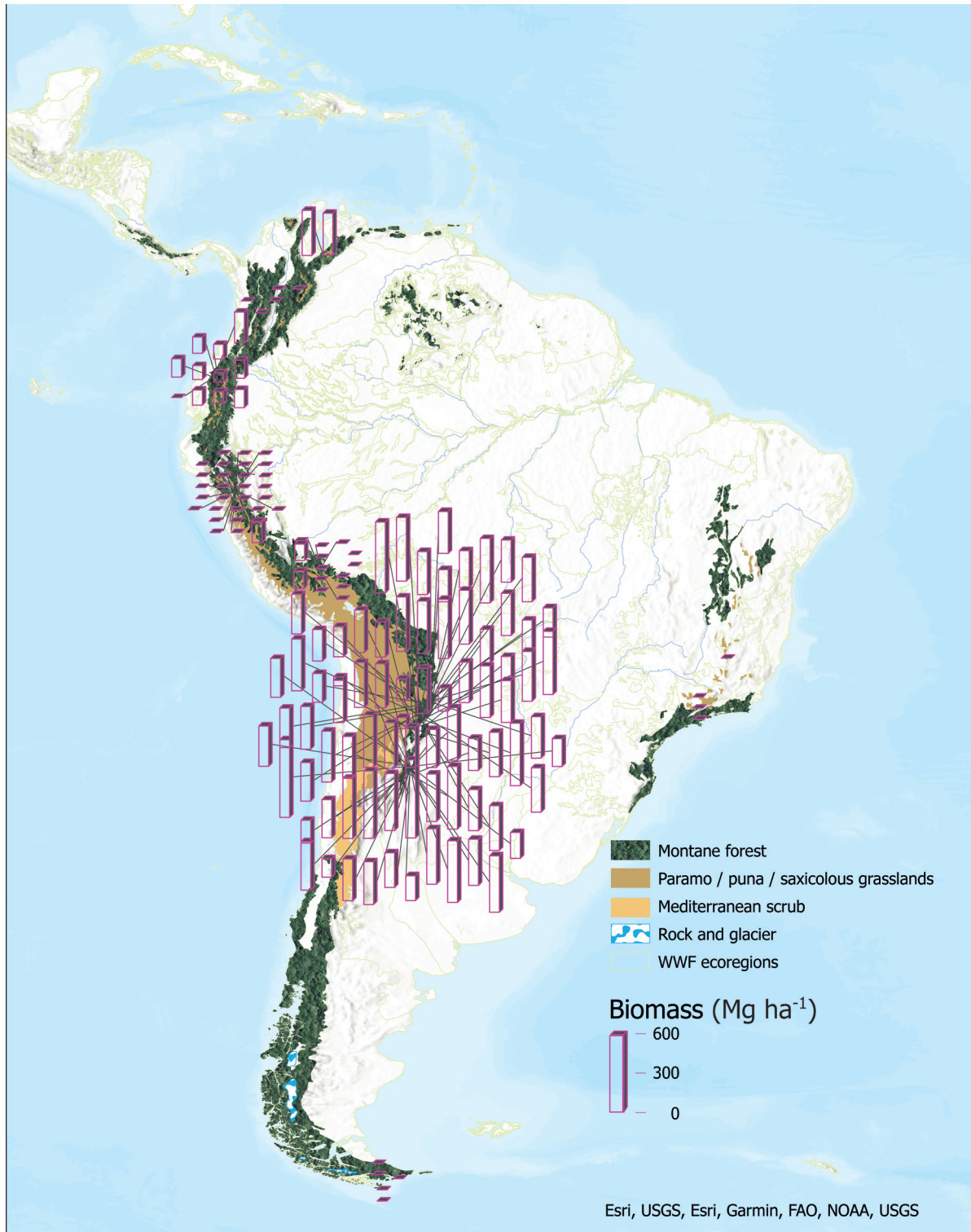


Figure 5. Biomass estimates (Mg ha^{-1}) in permanent plots established in montane forest at eight sites. For site information see Figure 1 and Table 2; horizontal line indicates plot location with no reported biomass.

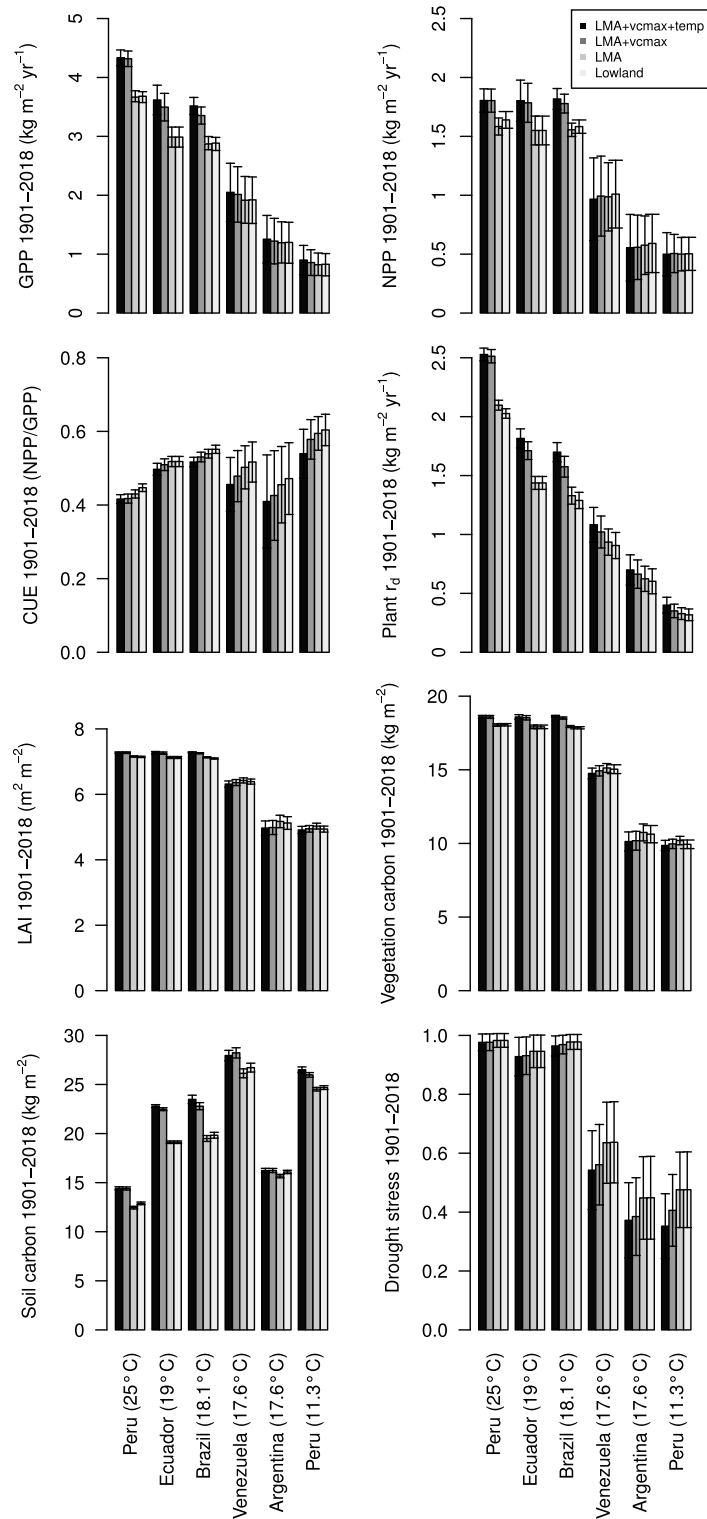


Figure 6. Selected outputs from the preliminary modelling using the DGVM-JULES. Temperature values in parentheses after each site are annual means. Peru, Tambopata lowland forest reference site; Ecuador, western Andes (Yanacocha Reserve); Brazil, Serra da Mantiqueira (Campos do Jordão); Venezuela, Mérida Andes (La Mucuy and La Carbonera); Argentina, Tucumán; Peru, Cusco upper montane forest site. For the description of the four simulations with different ecophysiological parametrisation of the model indicated in the legend see Table S2.

implications for regional variation in plant species assemblages and their community functional traits and ecophysiology. For example, the variable temperature sensitivity of lowland tropical forests

across continents has been shown by Sullivan et al. (2020), demonstrating that the sensitivity of primary production varied among continents and that the sensitivity of photosynthesis to temperature

used in process-based models was likely to be an overestimate. This suggests that montane-specific biophysical parameters additional to what GEM has already available (Malhi et al. 2021) may be necessary to realistically simulate processes in mountain ecosystems.

Second, there is a major lack of local climate data that are used in DGVMs and other process-based models. The lack of local data has direct implication for model outputs. Specialist workshops on mountain climate and modelling climate impacts on ecosystem services at the International Mountain Conference, Innsbruck, 2019, have concluded, among others, that (1) given the large uncertainties associated with mountain regions to properly validate climate models, there is a need for reliable observations at high spatial and temporal resolution; (2) the expectation regarding the accuracy and reliability of atmospheric data is not met by increased grid resolution alone without adjusting parameters such as turbulent exchange and radiation; and (3) there is a need to validate high-resolution regional climate models for additional variables other than temperature and precipitation so that they can be used in dynamic modelling of ecosystem services (<https://www.uibk.ac.at/congress/imc2019/program/>). In a South American context, there is an acute need for locally collected data series (see e.g. Carrillo-Rojas et al. 2019; Rodríguez-Morales et al. 2019) to increase the spatial precision of model projections and reduce uncertainties associated with mountain environments, partly attributable to different land use and land dynamic histories (e.g. Flantua et al. 2016). Table S4 contains the recommended variables that a site would require to measure/record, given local constraints, to satisfy minimum (priority level 1) to optimum (priority level 2) requirements for parameterising and testing DGVMs and other process-based models. Very few items listed in Table S4 were available for our simulation using JULES.

JULES-DGVM simulations

In our simulation, the decline with elevation in NPP from 1.5 and 1.8 to 0.5 kg C m⁻² year⁻¹ was similar to that reported by Girardin et al. (2010) along the Amazon – Andes transect of GEM from lowland evergreen rainforest (194 m a.s.l.) to upper montane forests in the Andes (3020 m a.s.l.). Their empirically derived values of NPP along the gradient from 1.4 kg C m⁻² year⁻¹ to 0.5 kg C m⁻² year⁻¹ are close to our modelled

values of NPP. Parametrising the model with montane-specific leaf and photosynthetic traits as opposed to traits for lowland tropical forests following Harper et al. (2016) and Bahar et al. (2017) resulted in the simulated CUE having a value closer to the observed values (<0.4; Marthews et al. 2012) in montane forest along the transect used and reported by Girardin et al. (2010). It is important to note that the montane-specific parametrisation (Bahar et al. 2017) we used in these simulations relied on published data from various montane sites, including non-neotropical sites.

Contrary to a previous modelling study along the Amazon – Andes GEM transect, which failed to adequately represent montane forests (Marthews et al. 2012), our preliminary simulations in JULES returned reasonably realistic trends in the relationship between temperature and physiological processes. The model by Marthews et al. (2012) used the dynamic vegetation module of Cox (2001) to model vegetation demographic processes in JULES and has resulted in poor model performance by underestimating the upper distribution of forest vegetation (i.e. the model simulated a die-back of the upper montane forest). In our study, a similar case was recorded in an exploratory gridded implementation of JULES – DGVM. Biomass values comparable to those found in puna (data not shown) were returned instead of values characteristic of montane forest in Peru where vegetation in the grid was not exclusively forest in the upper montane belt. Having reliable estimates of the climatic treeline – the TREELIM model, confirmed by local experts, estimated well treeline position – appears one feature that DGVMs need for use in high mountains.

Fyllas et al. (2017) have successfully simulated the biomass decline from the Amazon lowlands to the upper montane belt in the Andes, using an individual-based model that related plant trait turnover to changes in solar radiation along elevation using TFS. The approaches represented by JULES DGVM and TFS, while appear contrasting, are complementary. The underlying assumption in the work by Fyllas et al. (2017) was that a climate – vegetation relationship exists, and it can be quantified by the change in leaf traits along elevation that represents adaptation to the temperature gradient. In our preliminary JULES simulations, this adaptation component is missing, and there is a direct temperature–physiology relationship that is assumed to change photosynthesis, respiration and tissue growth allocation patterns (compare with Sullivan et al. (2020)).

It is known that the taxonomic composition changes from lowland to upper montane forest are conceivably accompanied by changes in functional leaf traits (see e.g. Llerena-Zambrano et al. 2021). Additionally, there is a change in life form composition, especially in the upper montane belt and most remarkably in the forest – alpine ecotone, with further changes in the alpine belt itself (Nagy et al. 2003; Nagy and Grabherr 2009; Körner 2021a). Undoubtedly, such changes in the distribution of taxonomic groups and life forms represent adaptations and not simply an instantaneous temperature dependency of physiological processes. Thus, the amalgamation of process and trait-based approaches holds a promise for the future development of vegetation models. There is ample scope for further empirical research evaluating the community-weighted functional trait composition change from lowland to alpine vegetation and its relationship with the temperature sensitivity of photosynthesis, respiration and growth in tropical mountains, as well as the potential impacts of hypobarism and hypoxia (Wang et al. 2017; Körner 2021a).

Modelling alpine vegetation above the treeline, using process-based models has received comparatively little attention. In South America, Biome-BGC has been used to estimate above-ground biomass and hydrological processes in the páramo in Ecuador (Minaya et al. 2016); the results projected a two-fold decrease in above-ground biomass between 4100 m and 4500 m elevation that overestimated but nonetheless agreed reasonably well with field data (Minaya et al. 2015). However, estimates of water fluxes were inaccurate, likely owing to the inaccurate estimators of soil, water storage, and evaporative processes. Elsewhere, modelling NPP with the use of Biome-BGC on the Tibetan Plateau (comparable to alpine vegetation in the subantarctic alpine vegetation in South America) has been reported by Sun et al. (2017 and references therein). An important consideration in mountain ecosystems is the large C stocks in the soils (see Box 1). A new version of Biome-BGC with 10 soil layers has recently been developed (Hidy et al. 2021) and is yet to be applied to mountain ecosystems.

Representation in DGVMs of processes in a mountain context

Related to the identified need for data is that it may be necessary to reconsider the representation of some of the processes developed for

lowland tropical forest when applying to mountain forests and alpine vegetation. Lowland tropical rain forests represent one end of a biophysical gradient from lowlands to high mountains with alpine vegetation/snowline. Along this gradient, largely related to climate, complex interactions of topography, hydrology, and soil processes (topo-hydro-pedo gradients, Nagy and Grabherr 2009) are manifest. How these factors may need to be represented to improve DGVMs for implementation in mountain environments requires further work. It appears that in a first step considerations could be given to characterise growth limitations other than the potential low-temperature limitation of photosynthesis. An adequate future representation in the model of growth limitation, be it caused by nutrient availability or by restriction of meristematic activity (Körner 2012), is likely to address this issue. An extensive body of empirical work points at the so-called sink limitation (new tissue formation to receive photosynthates) rather than the limitation of photosynthesis *per se* in trees at the upper end of montane forests (Fatichi et al. 2014). Modelling using sink limitation appears to improve biomass estimation at European tree-lines (Leuzinger et al. 2013) and Hayat et al. (2017) have recently presented a model of tree growth using C source and sink limitation, for potential inclusion in DGVMs. In addition to a focus exclusively on C (Malhi and Grace 2000; Sitch et al. 2008), potential limitations of coupled biogeochemical cycles (C, N and P) along the biophysical gradient that mountains represent, should be given attention to (Fatichi et al. 2014). The work by Jones et al. (2020), with the inclusion of a non-structural carbohydrate pool in the JULES-DGVM, is an important first step in this direction, and in any mechanistic approach to simulate treeline dynamics.

We reiterate again that there are numerous scale-related issues associated with applying DGVMs at the local and regional scales which are required to be resolved for their successful application to highly heterogeneous mountain terrain (see e.g. Bachelet et al. 2015). Local implementation of models and posterior upscaling in topographically diverse mountain environments is preferable to gridded implementation so as to reduce error owing to spatial heterogeneity unaccounted for (see e.g. Minaya et al. 2018 for biomass estimates

Box 1. Mountain specific challenges for modellers.**1. Some environmental variables change in predictable manner, others do not.**

Temperature and air density decrease in a predictable manner with elevation, but precipitation may increase, decrease or have combinations of increase/decrease with elevation (Figure B1) and thus, together with temperature can modify net primary productivity (NPP) and limits to tree growth (for a wind pattern-corrected precipitation model see (Karger et al. 2017)). Temperature lapse rate, typically 6.5 K km^{-1} (Nagy and Grabherr 2009; Körner 2021a), in the presence of sufficient humidity may be used to define the elevation limits of tree growth worldwide, empirically determined at a mean growing season temperature of ca. 6.5°C (Körner and Paulsen 2004; Paulsen and Körner 2014). In addition to elevation, site temperature is a function of latitude, thus, cold-limited treelines, if were not affected by precipitation patterns, would decline in a regular manner from the equator towards the poles.

2. Extensive mountain ranges may be exposed to various macroclimates and in turn determine regional climate by creating orographic rain shadows.

The Andes run from north (8° N) to south (55° S), spanning ca. 63 degrees latitude and present complex climate patterns along its length and across its two climatically contrasting macroslopes (Pacific and Atlantic; Garreaud and Aceituno 2007; Nagy and Grabherr 2009; Marengo et al. 2011). Both macroslopes of the Andes, in a spatially disjunct manner, contain an amplitude in precipitation that ranges from ever wet to arid/hyper arid (Garreaud and Aceituno 2007). There are large differences in precipitation in south-eastern Brazil between the maritime Atlantic coastal range flanking the Atlantic coast and the interior rain shadow affected ranges. Temperature in most of the Andes is low enough at high elevations to limit tree growth and result in alpine vegetation. In contrast, the south-eastern Brazilian mountain ranges do not rise high enough to reach temperature limitation of the tree life form.

3. Climate change holds many challenges for empirical scientists and modellers alike.

During the last Ice Age, there was an extension of ice caps on the high mountains of the Andes and a compression of mountain vegetation belts (Clapperton 1993); a number of montane forest species are thought to have descended from the montane forests of the Andes into the Amazon lowlands and then retreated to the Andes with the Holocene warming (Bush et al. 2011; Bush and Gosling 2012). It has been suggested that in some parts of the south-eastern Brazilian mountain ranges the existence today of non-forest vegetation is the result of past glacial – interglacial cycles (and of a certain lag in their recolonisation by forest; Behling 1997, 2008) and Holocene tectonic events, perhaps triggered by climate extremes (Modenesi-Galettieri 2000). In recent times, a warm-edge range contraction in some high elevation tree species has been reported (Feeley 2012; Duque et al. 2015), suggesting a strong response to recent warming. Equally, there has been evidence for an increase in the upper elevation limit of potato cultivation in the central Andes (Halloy et al. 2006) and a putative range extension in some tree species (Fadrique et al. 2018). Projected climate change has numerous implications (Magrin et al. 2014; Nagy et al. 2018) for mountain ecosystems. They range from changes in the geographical range of species (Ramirez-Villegas et al. 2014), composition and extent of cover of vegetation types (see e.g. non-analogue communities in non-analogue climates; Williams and Jackson (2007)) to impacts on hydrology (Vuille 2013) that will result from the melting of glaciers and from the changes in the quantity and pattern of precipitation (Marengo et al. 2011), and its implications for ecosystem services and resulting policy responses (Cuesta et al. 2019). Plant migration and acclimation/adaptation processes need to be included in dynamic global vegetation models (DGVMs) to correctly represent vegetation range expansion and contraction in mountain ecosystems. Acclimation and adaptation of photosynthesis have been included in the Joint UK Land Environment Simulator (JULES)-DGVM, however this is based on a global datasets with sparse data in tropical ecosystems (Mercado et al. 2018).

4. Dissected mountain topography causes large spatial variability in biomass.

Biomass variability related to topography in mountain landscapes requires careful consideration (Homeier et al. 2010; Sattler et al. 2014) for accurate estimates of carbon (C) stocks. As deforestation, secondary forest regrowth and forest plantations will continue to characterise mountain ecosystems, it is essential to have ground-based biometric and species trait data (Lohbeck et al. 2015; van der Sande et al. 2016) of old-growth, secondary and plantation forests to adequately parametrise and calibrate DGVMs so that remotely sensed information regarding biomass and vegetation C estimates and potential ecosystem service value estimates can be improved.

5. Climate and land use and land cover change are interrelated, and land use change today is affected by increased mobility of the rural population.

Land use as well as natural vegetation cover in the Andes has a long history (Ellenberg 1979) and largely been determined by limiting climatic factors (for the Mérida Andes, Venezuela see Monasterio (1980)) and by the availability of water for irrigation in areas with water limitation (Denevan 2001). The páramo and puna (Grau et al. 2018) have been pastured both pre- and post-Columbian times (Sylvester et al. 2017). Recent conversion into pasture or other uses has affected large expanses of montane forest in the Andes (Navarro and Maldonado 2002; Armenteras et al. 2010, 2017) and have resulted in large losses of vegetation and soil C stocks, they have suffered displacement by recurring erosion or have been consumed by the use of fire. The tendency for conversion has been maintained and reinforced in densely populated areas, such as in the coastal mountain ranges of south-eastern Brazil (Ribeiro et al. 2009; Tabarelli et al. 2010) and in lowland and submontane forests in the Andes (Aide et al. 2019). Recent large-scale exodus of the population from many remote Andean rural areas has resulted in regrowth of secondary forest on abandoned agricultural land (Grau et al. 2007; Aide et al. 2019). This is clearly reflected in the fact that many montane forest plots in the Andean Forest Plot initiative are in fact in secondary forests (Malizia et al. 2020). Biomass accumulation in secondary forests (Poorter et al. 2016) has a different dynamic from that in old-growth forests (Sullivan et al. 2020). However, while knowledge on the dynamics of old growth vs. secondary forests is beginning to become available for lowland tropical environments, there is less information available for montane forests (Calderón-Loor et al. 2020; Blundo et al. 2021; Duque et al. 2021; Quintero 2021).

6. There is much carbon in mountain vegetation, but not all of it is in the trees.

Although the role of montane forests in C sequestration has been undervalued for their perceived smaller biomass (Figure B2) per area and smaller areal extent than those of lowland forests (Brujinzeel and Veneklaas 1998), but see Spracklen and Righelato (2014), montane forests present an important feature whereby the smaller above-ground tree biomass C can be compensated by increased below-ground biomass and soil C storage (Girardin et al. 2010; Moser et al. 2011). There are also extensive peatlands (locally known as bofedales) above the treeline in the Andes (Cooper et al. 2010; Hribljan et al. 2015, 2016, 2017; Oyague and Cooper 2020). Despite their long history of grazing (Hofstede et al. 1995, 2002; Buytaert et al. 2006), these ecosystems represent important C sinks (but see Carrillo-Rojas et al. (2019)), whose strength may be related to past and current land use (Rolando et al. 2017, 2017; Madrigal-Martínez and García 2019; Calderón-Loor et al. 2020), and recent climate change impacts (Dangles et al. 2017; Cuesta et al. 2019). Páramo and puna also contain important quantities of C. The treeline ecotone in an upper montane forest – puna transition zone has been reported to store between $127 \pm 8 \text{ Mg C ha}^{-1}$ (puna) and $195 \pm 6 \text{ Mg C ha}^{-1}$ (forest), with their soil C 119 ± 8 and $118 \pm 15 \text{ Mg C ha}^{-1}$ being equal (Gibbon et al. 2010); the values reported by Zimmermann et al. (2010) for soil across the treeline in Peru were $118 \pm 15 \text{ Mg C ha}^{-1}$ and 119 ± 8 to $147 \pm 14 \text{ Mg C ha}^{-1}$. Corresponding values in the Ecuadorian páramos (Yanacocha watershed, treeline 3900 m; forest 3600–3900 m; páramos 3900–4300 m) have been reported at ca. 139 Mg C ha^{-1} (of which 113 Mg C ha^{-1} in the soil) in the páramo and 111 Mg C ha^{-1} (64 Mg C ha^{-1} in the soil) in secondary forest regrowth (Calderón-Loor et al. 2020). Soil C values in the soil (0–30 cm) under various land uses in the Peruvian puna have been found to range between 123 ± 4 and $136 \pm 4 \text{ Mg C ha}^{-1}$ (Rolando et al. 2017), similar to those reported by Gibbon et al. (2010). High Andean wetlands contain the largest amounts of soil C in peat, whose depth may reach 10 m. Deep cores (5–10 m) in Bolivia have indicated peat C stocks between 572 and 1040 Mg C ha^{-1} (Hribljan et al. 2015), while in Ecuador C stocks to a depth of 3.8 m have been estimated at $1282 \text{ Mg C ha}^{-1}$ (Hribljan et al. 2016). The importance of high-elevation wetlands is highlighted by the fact that in Ecuador the amount of C stored in peat may be equivalent to nearly 25% of all forest biomass C stocks (Hribljan et al. 2017). Thus, climate change and land use change may cause the release of considerable amounts of CO_2 . The biogeochemical model Biome-BGCMuSo with its multiple soil layers appears a particularly good choice to model soil C and below-ground vegetation C.

Environmental factors limiting plant growth on mountains

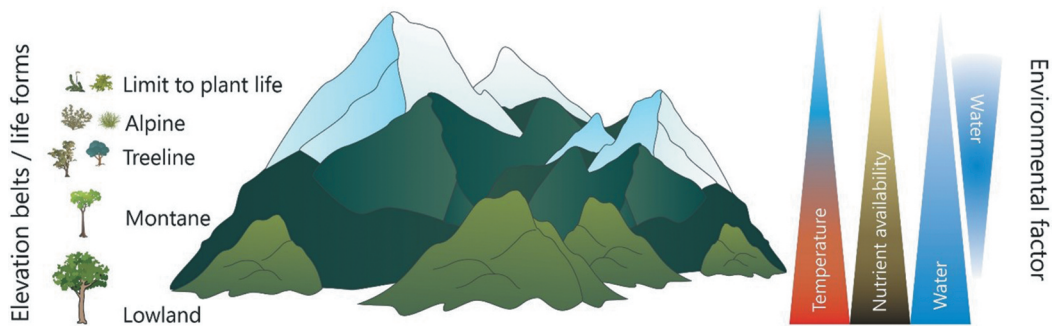


Figure B1. Elevation in mountains is associated with gradients in potential growth limiting factors. There is a relatively consistent lapse rate in temperature (ca. 6.5 K km^{-1} decrease); nutrient availability for plants varies with underlying geology; however, nutrient availability for plant uptake generally decreases along the temperature gradient from lowlands to the upper limit of plant life. Precipitation trends with elevation vary with geographic position; they may diminish, increase, or follow a combination of trends in increase and decrease. Temperature, and water and nutrient availability together are important for the observed elevation patterns of the distribution of plant life forms and plant functional traits, which, in turn, may be related to plant growth limitation. The partial pressure of CO_2 of the atmosphere remains constant with elevation, while the amount of light and its quality are related to cloud formation (geographical position). Light and CO_2 concentration have been shown empirically not to limit growth (they may limit photosynthesis, as evidenced by light and CO_2 curves vs. photosynthetic capacity). Meanwhile, temperature and the availability of nutrients and water may limit plant growth (meristematic activity and tissue formation), in the absence of limitation of photosynthesis. To successfully apply Dynamic Global Vegetation Models (DGVMs) to mountain environments the models need to represent in their structure and parametrisation the specificities of mountain environments. For a detailed treatment of growth (sink) limitation and its potential use in DGVMs see e.g. Fatichi et al. (2014). Graphics are courtesy of the Integration and Application Network (ian.umces.edu/media-library).

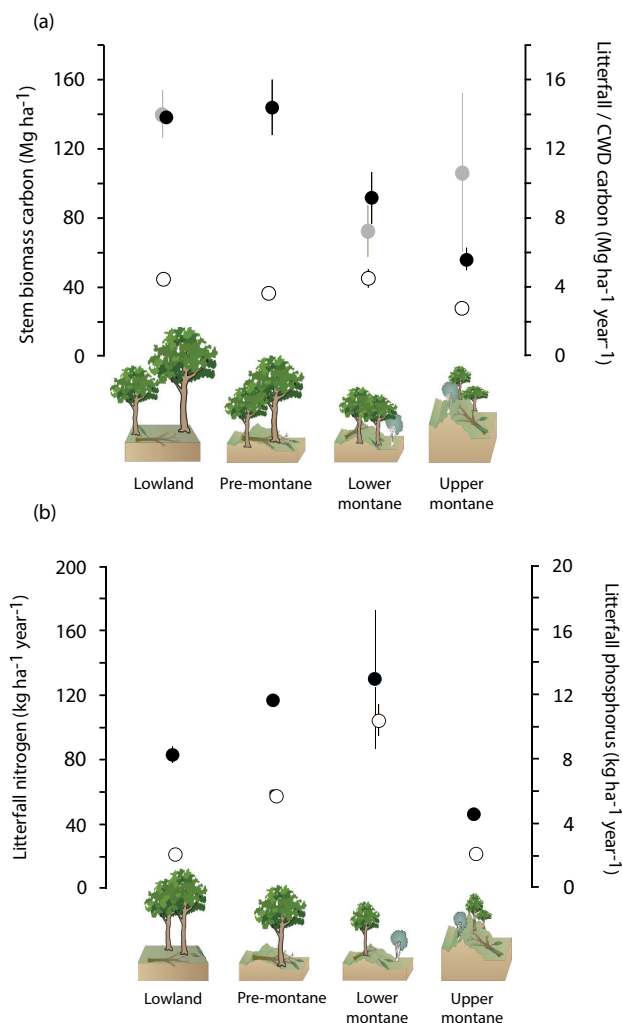


Figure B2. Carbon density estimates reported in tropical lowland evergreen forest in the Amazon basin and in montane forest on the Atlantic macroslope of the Andes: open black circle, litterfall; filled grey circle, coarse woody debris (CWD); filled black circle, stem biomass (a). Annual return of litterfall nitrogen (filled circle) and phosphorus (open circle) for the same forest types (b). Modified after Buscardo et al. (2016).

using Biome-BGC in the páramo). Where justified by the need and available resources, a landscape-scale representation would be desirable. The importance of the sensitivity of projection to spatial resolution has also been shown for niche models applied to mountain environments where estimates of species extinction rates at a coarse resolution (0.5 deg. \times 0.5 deg.) overestimated several fold (Thuiller et al. 2005) the extinction rates projected at fine resolution (25 m \times 25 m) in alpine vegetation (Randin et al. 2009). Gridded implementation usually uses a resolution far too coarse for mountain environments as grids poorly account for the third dimension that mountains represent, and this results in underestimates of area, with consequent implication for error propagation in all subsequent estimates and applications. These are also important considerations for plant migration which is a major challenge for DGVMs (Lehsten et al. 2019).

Model projections including dynamic social-ecological scenarios

For an ESM to be meaningful in the context of South American mountain ecosystems, it requires an adequate DGVM component based on local and regional parametrisation, and data to allow verification in the field. Importantly, the use of DGVMs must be complemented by plausible scenarios regarding the use of ecosystem services (Spangenberg et al. 2014). Such scenarios are often built on broad theoretically conceived narratives, in relation to a baseline ‘business-as-usual’ scenario (Spangenberg 2007; Tallis et al. 2018). Scenarios based on stakeholder consultation of land management and using companion modelling (Étienne et al. 2003; Étienne 2014) offer a more realistic way of projecting changes in potential ecosystem services and their uses (Alonso-Betanzos et al. 2017), and model and monitor sustainable resource use. Therefore, the use of DGVMs is recommended to be implemented as an integral part that encompasses the biophysical component (drivers, structure and functioning of ecosystems) of local and regional social-ecological systems (Collins et al. 2011; Díaz et al. 2015) so that projections of future changes in the C cycle in South American mountains and their impacts on the Earth System may be more accurate and realistic. Past social-ecological dynamics, reconstructed from palaeo and archaeological data (e.g. Gosling and Williams 2013) may hold useful consideration for the temporal

dynamics of social-ecological systems of the South American mountains.

The proposed network

The proposed network is to complement the existing Andean Forest Network (Malizia et al. 2020) and GEM Amazon – Andes transect (Malhi et al. 2021) by (1) extending them to extratropical latitudes along the Andes and to mountain ranges outside of the Andes in South America and (2) extending the scope of field investigations so that empirical data could be used to underpin DGVMs and other process-based models.

We propose an initial network of nodes of mountain research sites that represent diverse climates (temperature and precipitation gradients), biogeography and land use histories (Figure 1; Table 2) to exploit existing information and fill the identified gaps in data availability for producing baseline knowledge for better DGVMs that locally and regionally can be used to inform management decisions for mountain ecosystems and related ecosystem services. The network will facilitate coordination, integration and synthesis for existing sites regionally and internationally and to foster multi-site analyses and synthesis of current status and trends of global change on mountain ecosystems. We aim at establishing common protocols for mountain ecosystem observations by adopting protocols from existing initiatives (<http://gem.tropicalforests.ox.ac.uk/>) to satisfy modelling needs (Table S4). Homogenising existing long-term data sets, such as, for example, historic climate data, in order to analyse current and future impacts of global change on different mountain ecosystems in South America is a priority and has already started (see e.g. daily data for 1973–2000 at the Campos do Jordão site). Importantly, the network has initiated establishing core sites with instrumentation, such as installing automatic weather stations and establishing facilities for the measurement of fluxes of energy and matter (Site 6, Omora Park, Chile; Site 7, Campos do Jordão, Brazil).

The proposed network will create novel synergies through international collaborations that will lead to broadening the current scope in empirical field research and vegetation modelling, beyond lowland tropical forests, to include montane forests and treeless ecosystems, and will establish the basis for a long-term collaboration between empiricists and modellers. The network is expected to significantly improve our modelling

capabilities, e.g. by using existing empirical knowledge for revising model parameters, to define plant functional types to represent montane forests and treeless alpine vegetation, and improve relevant process representations in DGVMs, specifically JULES and its new plant successional scheme (Robust Ecosystem Demography, RED; (Argles et al. 2020)). The results can then be applied to the UK ESM for coupled land-climate projections, and IPCC assessments, in addition to their use in local and regional planning for sustainable use of ecosystem services.

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