

INVITED REVIEW

Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems

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- **Background** Earth system models describe the physical, chemical and biological processes that govern our global climate. While it is difficult to single out one component as being more important than another in these sophisticated models, terrestrial vegetation is a critical player in the biogeochemical and biophysical dynamics of the Earth system. There is much debate, however, as to how plant diversity and function should be represented in these models.
- **Scope** Plant functional types (PFTs) have been adopted by modellers to represent broad groupings of plant species that share similar characteristics (e.g. growth form) and roles (e.g. photosynthetic pathway) in ecosystem function. In this review, the PFT concept is traced from its origin in the early 1800s to its current use in regional and global dynamic vegetation models (DVMs). Special attention is given to the representation and parameterization of PFTs and to validation and benchmarking of predicted patterns of vegetation distribution in high-latitude ecosystems. These ecosystems are sensitive to changing climate and thus provide a useful test case for model-based simulations of past, current and future distribution of vegetation.
- **Conclusions** Models that incorporate the PFT concept predict many of the emerging patterns of vegetation change in tundra and boreal forests, given known processes of tree mortality, treeline migration and shrub expansion. However, representation of above- and especially below-ground traits for specific PFTs continues to be problematic. Potential solutions include developing trait databases and replacing fixed parameters for PFTs with formulations based on trait co-variance and empirical trait–environment relationships. Surprisingly, despite being important to land–atmosphere interactions of carbon, water and energy, PFTs such as moss and lichen are largely absent from DVMs. Close collaboration among those involved in modelling with the disciplines of taxonomy, biogeography, ecology and remote sensing will be required if we are to overcome these and other shortcomings.

Key words: Plant functional types, PFT, Earth system model, ESM, Arctic tundra, biogeography, dynamic vegetation models, global change, plant traits, high-latitude ecosystem.

INTRODUCTION

Scientists have long sought to capture the spatial and temporal behaviour of coupled Earth systems through experiments, observations and the incorporation of knowledge gained from those efforts into simulation models (Luo *et al.*, 2011; McCarthy *et al.*, 2012; LeBauer *et al.*, 2013). Recent decades have seen a rapid evolution in our ability to simulate, using computer models, a variety of processes including biogeochemical cycles of carbon and nitrogen; water and energy transfer among the biosphere, atmosphere and hydrosphere; and atmospheric and ocean thermal behaviour and circulation patterns (Friedlingstein *et al.*, 2006; Chapin *et al.*, 2008). It is now widely accepted that representation of these and many other processes in models that couple the land surface, atmosphere and oceans is important, especially when such models are being used to project future climate change scenarios and associated uncertainties (Stainforth *et al.*, 2005).

Earth system models (ESMs) are sophisticated simulation tools that describe, through equations, algorithms and appropriate parameterizations, the properties and processes that govern interactions among components of the Earth system (Murphy *et al.*, 2004). The development and use of ESMs have promoted a holistic study of coupled land–atmosphere–ocean systems and, as a result, have improved our understanding of their many interdependencies. Uncertainties in climate predictions, however, can arise from insufficient knowledge of the physical, chemical and biological mechanisms involved in the climate system and from insufficient representation of land surface processes given variation in soils and vegetation types, and consequences for ecosystem structure and function. While it is difficult to single out any one component as being more important than another in these complex models, terrestrial vegetation is a critical player in the dynamics of the Earth system (Snyder *et al.*, 2004; Bonan, 2008) and among the largest sources of uncertainty in climate change predictions (Friedlingstein *et al.*,

2006; Moorcroft, 2006; Denman *et al.*, 2007). In this context, improved process representation is an active area of study, and increased attention is being paid to better understanding and describing biophysical and biogeochemical interactions that couple the vegetated land surface to the atmosphere through energy transfer and carbon, nutrient and water cycles (Chapin *et al.*, 2008; Thornton *et al.*, 2009).

Dynamic vegetation models (DVMs) were designed to represent important structural and functional variables that together control land-surface energy, carbon, nutrient and water budgets (Cramer *et al.*, 2001; Bonan, 2008). Their development was conceptualized as a way to understand the factors that influence the distribution of vegetation (Prentice *et al.*, 2007). As a strategy for representing the complexity of nature in models (Woodward, 1987; Kittel *et al.*, 2000), the plant functional type (PFT) concept has been applied as a tool in modelling the effects of global change on the terrestrial biosphere (Cramer *et al.*, 2001; Prentice *et al.*, 2007). This concept has proven useful in simulations of plant distribution and climate change research at regional to global scales (Haxeltine and Prentice, 1996; Foley *et al.*, 1998; Kittel *et al.*, 2000; Cramer *et al.*, 2001; Bonan *et al.*, 2002, 2003; Sitch *et al.*, 2008). This field, however, is changing rapidly as scientists consider options for representing plant diversity in models, and ensuring that once incorporated into models the resulting sources of uncertainty can be identified and, where necessary, resolved or reduced (Reu *et al.*, 2011a, b; Pavlick *et al.*, 2013; Scheiter *et al.*, 2013). There is mounting evidence that uncertainty can arise from several sources, including incorrect or incomplete PFT classifications and inadequate PFT parameterizations. van Bodegom *et al.* (2012) argue that a challenge for modellers and ecologists alike is to consider the consequences of traditional fixed parameterization of PFTs and, if warranted, move towards a flexible trait-based approach, which would allow PFTs to occupy the landscape based on how plants with different trait combinations (i.e. co-variation of traits) perform in a given environment. Inclusion of trait variation within PFTs has been shown to have profound impacts on predicted carbon fluxes and vegetation distribution (Verheijen *et al.*, 2013).

While PFTs are important for characterizing vegetation dynamics and their Earth system implications at the global scale, they are also a useful construct at landscape and regional scales. The role of PFTs in helping to characterize vegetation responses to changing environmental conditions is particularly important for biomes found at northern high latitudes, specifically the Arctic tundra and the boreal forest (taiga). These ecosystems have been especially sensitive to changing climate over the past several decades (Bhatt *et al.*, 2010; Beck and Goetz, 2011; Dutrieux *et al.*, 2012; Xu *et al.*, 2013). Recent observations from satellites indicate a widespread ‘greening’ of Arctic tundra (Bhatt *et al.*, 2010), caused in large part by shrub expansion (Myers-Smith *et al.*, 2011), along with some ‘browning’ observed in parts of the boreal forest (Beck and Goetz, 2011), most probably caused by local to large-scale tree mortality (Hogg *et al.*, 2008; Michaelian *et al.*, 2011). Not all high-latitude ecosystems have responded similarly to climatic changes over time (de Jong *et al.*, 2012), and distinct responses are observed among evergreen trees, deciduous trees, erect and prostrate shrubs, evergreen and deciduous shrubs, graminoids, forbs, mosses and lichens (Beck and Goetz, 2011; Fraser *et al.*, 2011;

Buizer *et al.*, 2012; Elmendorf *et al.*, 2012a; Ropars and Boudreau, 2012; Villareal *et al.*, 2012; Frost *et al.*, 2013). Because of the unique biological, physical and chemical effects that each of these vegetation types has on ecosystem characteristics, closer scrutiny regarding how models represent vegetation will be necessary to answer broad, regional-scale questions.

In this review, we explore these topics by (1) examining the origin of the PFT concept; (2) assessing lessons learned as the PFT concept has been integrated into DVMs operating at regional scales for northern high-latitude ecosystems; (3) identifying areas in the representation and parameterization of PFTs where recent improvements have been made, and where key challenges remain for future improvement; and (4) evaluating capabilities for monitoring, mapping and validating current and projected patterns of vegetation dynamics using satellite- and aircraft-based remote-sensing and ground-truthing techniques. Finally, (5) we address if and how these many conceptual and technological advancements have enhanced our capabilities to predict ongoing patterns of rapid vegetation change in northern high-latitude ecosystems. Several of these areas have played a key role in the development of DVMs and will continue to do so in the foreseeable future. However, we anticipate that certain aspects of this endeavour will change, including an increasing emphasis on remote sensing and trait databases, and a shift from fixed to variable parameterization of PFTs (Fig. 1).

ORIGIN AND EARLY USE OF THE PLANT FUNCTIONAL TYPE CONCEPT

The concept of basic plant types developed long before the current interest in PFTs as a modelling construct. As early as the 19th century, plant types defined entirely by structure, such as broad-leaved trees, stem-succulents or graminoids, had been called growth forms (*Wuchsformen* or *Hauptformen*) based on classification strategies by von Humboldt (1806), Grisebach

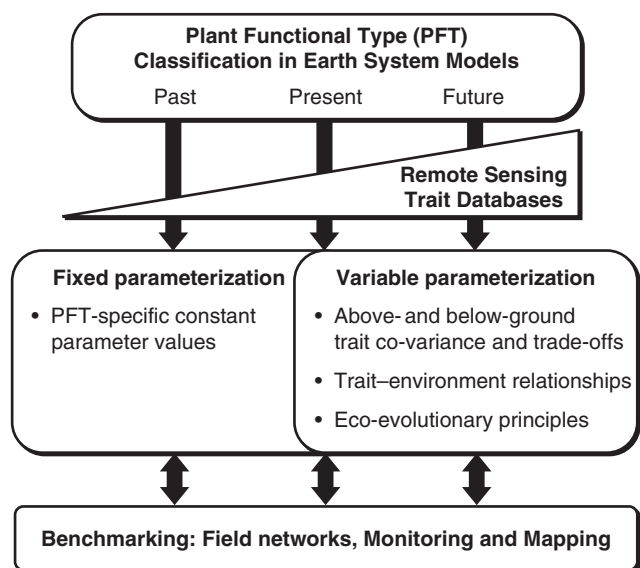


FIG. 1. A conceptual diagram showing critical aspects of PFT classification, remote sensing, trait databases and methods of PFT parameterization that will be important as DVMs develop into the future.

(1872) and others (Drude, 1896; Barkman, 1988). Structural types interpreted as ecologically significant adaptations to environmental conditions were called life forms (*Lebensformen*) by Warming (1895) and could be interpreted as basic ecological types, grouping taxa with similar form and ecological requirements. Growth forms and life forms both provide a convenient way of describing vegetation structure without having to treat large numbers of species individually (Schimper, 1898; Rübél, 1930; Schmithüsen, 1968; Walter, 1968, 1973). The term ‘functional’ in connection with modern systems of plant types was perhaps first used in the ‘plant functional attributes’ of Gillison (1981).

The first global classification of integrated plant types for modelling purposes was the ‘ecophysioognomic’ forms of Box (1981a), which were structurally defined based on broad morphological characteristics (e.g. trees, shrubs and grasses), but interpreted explicitly as environmental adaptations based on hypothesized form–function relationships. The idea to use such plant functional forms within a global model of vegetation growth was proposed as early as the 1980s (Box, 1980, 1981b, 1984). Implementation could not be pursued at that time due to various conceptual and computational limitations, but the idea of basic plant types was eventually adopted by global modelling efforts (Cramer and Leemans, 1993; Foley, 1995; Cramer, 1997; Peng, 2000). The term ‘plant functional type’ and its introduction to the general modelling community seems to have originated just before ‘A Meeting on Global Vegetation Change’, held at the International Institute for Applied Systems Analysis

(IIASA) in Laxenburg (Austria) in April 1988 (Prentice *et al.*, 1989; GCTE, 1991; Steffen *et al.*, 1992; Solomon and Shugart, 1993).

As the concept of PFTs developed and was eventually adopted for modelling vegetation dynamics, there arose three different conceptualizations (Box, 1995a): (1) the ‘form follows function’ approach of Box (1981a); (2) an approach based purely on plant physiology, without reference to form; and (3) an approach seeking similarity of plant responses to increasing atmospheric CO₂ concentrations and higher temperatures (Smith *et al.*, 1993; Potter and Klooster, 1999; Pausas and Austin, 2001). The third conceptualization makes no reference to plant form but has been held up as the ‘holy grail’ of plant functional modelling (Lavorel *et al.*, 2007), although no general, globally applicable set of purely ‘functional’ types has been developed.

The notion that form follows function (Box, 1981a) is apparent, with the structural controls on photosynthesis being a rather straightforward example. However, one might ask which traits or characteristics are most useful for representing PFTs in order to model important ecosystem processes of carbon, nutrient and water dynamics. Experience (Box 1981a, 1987, 1995a, 1995b, 1996) and recent statistical evidence (Douma *et al.*, 2012) suggest that the most important characteristics (Table 1) involve aspects of (1) plant size, especially relative to other plants; (2) plant permanence, especially woody vs. non-woody structure, but also aspects related to root longevity; (3) plant architecture, as expressed by growth form and branching pattern; (4) leaf form, as captured by leaf size and shape as

TABLE 1. Main characteristics for identifying plant functional types

Characteristic	Functional significance
Plant size	Ability to capture and control resources at the site (cf. respiration requirements of greater biomass)
Permanence of structure	
Woody vs. herbaceous	Support; water loss; potential for water uptake and for photosynthesis; permanent occupancy of space (cf. competition, especially in springtime)
Annual/perennial	All-or-nothing colonization strategy vs. storage and growth
Evergreen/deciduous	Use of whole growing season; competition vs. stress tolerance strategy
Root turnover/longevity	Investment in opportunistic vs. reliable water and nutrient uptake
Architecture	
Root/shoot ratios	Ratio of water-loss to water-uptake surface areas; re-growth reserves
Branching height	Taller growth if single main stem: greater control over available light
Branching pattern	Potentially taller if monopodial (with side branches), greater leaf area
Root spread/depth	Opportunistic vs. reliable water and nutrient uptake
Suffrutescence, etc.	Permanent root system for water uptake and re-sprouting
Leaf form	
Leaf size	Potential light capture (photosynthesis) vs. overheating (water loss)
Leaf shape	Control over water loss and internal hydration
Leaf structure	
Surface ‘hardness’	Control over water loss (vs. potential photosynthetic rate)
Chlorophyll density	Shade tolerance vs. light requirements
Metabolism	
Photosynthetic pathway	Enhanced photosynthesis in hot (C ₄) or dry (CAM) environments; reduction of photorespiratory losses
CO ₂ requirements	Response to CO ₂ enrichment (cf. tissue C:N ratios)
Reproduction	
Fruit size/number	Dispersal strategy
Seed size/number	Colonization vs. investment strategies
Phenology	
Re-sprouter/non-sprouter	Relationships with pollinators; timing of dispersal (cf. climate)
Vegetative spread	Re-growth after severe loss of above-ground biomass
	Reproduction under differing conditions; re-growth potential

Most aspects of plant function are related to plant form, and most of the characteristics listed here are structural. Some important aspects of plant function, however, do not have form manifestations.

biophysical regulators of water loss and carbon uptake; (5) leaf structure, including specific leaf area and shade tolerance; (6) metabolism as expressed by photosynthesis and respiration; (7) reproduction as expressed by dispersal strategy, propagation; and (8) plant seasonal activity (i.e. phenology), which may be much more complex than just evergreenness or deciduousness. Note that most current PFT classifications as applied in global and regional DVMs consider most of these aspects, but in very coarse categorical terms.

Basic plant structure involves not only permanence of above-ground biomass (woody vs. herbaceous), leaf longevity (evergreen vs. deciduous) and leaf structure (broad-leaved vs. needle-leaved), but also aspects of below-ground architecture and longevity (i.e. turnover). Plant size has implications for resource acquisition and growth, as well as for competition with other plants. The size, shape and shade tolerance of leaves are central to plant metabolism and water balance. For example, compound leaves with smaller individual leaflets can be deployed rapidly, provide greater ventilation and reduce overheating, thus aiding survival or maintaining favourable carbon and water balance in warm climates. Metabolism is also related to the consistency ('hardness') of the photosynthetic surface, light requirements and shade tolerance. Leaf structure involves functional trade-offs, especially between the higher photosynthetic rates per unit leaf area of 'softer' deciduous leaves and rates of water loss, nutrient use and utilization of the available growing season. These fundamental trade-offs can be circumvented or at least ameliorated by other adaptations, such as phenological variability. Plants in seasonally dry or cold climates often produce soft leaves with high rates of photosynthesis and simply drop them in the unfavourable season, greatly reducing water loss as well as respiration. Although plants in non-seasonal tropical rain forests may actually be 'ever-growing', most evergreens, including conifers, drop old leaves all at once, normally in springtime, just as new leaves are being produced.

Important plant characteristics are expressed not only in growth form, but also in species tolerance to prevailing environmental limitations. Some of the main limitation mechanisms for plants growing under high-latitude (or high-altitude) conditions are summarized in Table 2 (Box and Fujiwara, 2012). Although summer temperature thresholds and total degree-days are important for growth and survival, one of the basic limitations in northern latitudes involves cold temperatures (Walter and Weismann, 1938; Levitt, 1957, 1980). Range limits due to winter cold may be controlled by mean temperatures near or below freezing, persistent below-freezing temperatures or

one-off extreme-cold events. Summer precipitation usually is not limiting in many Arctic and boreal areas, but winter moisture may be needed, especially snow for buffering short evergreen taxa against extreme cold, or for extending the spring snowmelt season to ensure permanently moist conditions throughout the growing season. Most taxa are dormant in winter, so saturated soil is not a problem; most taxa do, however, require both soil moisture and aeration during the growing season. Most plants are not physically damaged until frost occurs, and even most temperate-zone plants, including evergreens, can tolerate some ice formation in the fluids within the relatively large space between cells. Higher plants, however, cannot survive significant ice formation in the fluids inside cells, because this results in mechanical damage to the cells themselves. Ice begins to form inside the cells of even relatively thick evergreen leaves at about -15°C , so this cardinal temperature, even over short durations, represents a limit for most broad-leaved evergreen trees and shrubs (Sakai, 1971; Larcher, 1973; Woodward, 1987). Deciduous trees and shrubs tolerate much colder conditions, but eventually ice may form inside the cells of their woody branches and trunks, depending on wood structure. Trees with ring-porous wood, i.e. with most of the active water-conducting structure concentrated in the outer wood from the most recent growing seasons, are vulnerable to lethal ice formation beginning at around -40°C (George *et al.*, 1974). On the other hand, trees with diffuse-porous wood, such as birches and other 'boreal' deciduous trees, can tolerate even lower temperatures, as can boreal conifers, due to their quite different wood structure (Archibold, 1995).

While the complexity of biological systems, encompassing many structural and functional characteristics of plants, may seem overwhelming, it is just these traits and their diversity that are used to define and, more importantly, differentiate PFTs in a wide variety of regional models. Such classification schemes provide a valuable starting point for assessing the diversity of plant types that need to be included in DVMs.

LESSONS LEARNED FROM MODEL SIMULATIONS OF VEGETATION DYNAMICS IN ARCTIC AND BOREAL ECOSYSTEMS

Early biogeographical models predict the distribution of potential vegetation assuming equilibrium conditions between climate and vegetation exist (Peng, 2000; Prentice *et al.*, 2007). This approach is intended for large-scale applications as it ignores dynamic processes. More recently, there has been an

TABLE 2. Main climatic limitations for plants in northern higher latitudes

Factor	Aspect and possible variables for representation in models
Warmth	Threshold for mean summer temperature or temperature sum for growing season
Coldness	Lower limits for mean temperature during coldest period, mean winter temperature minima and absolute minimum temperature
Moisture	
Total	Minimum annual precipitation requirement or minimum moisture balance (P/PET)
Seasonal	Winter precipitation needs or winter P/PET need (cf. spring snowmelt and permanent growing-season moisture)
Snow depth	Minimum need (for protection against cold) or maximum tolerance (cf. length of snow-free period)
Soil aeration	Requirement for aerobic root functions
Growing season	Minimum length for fruit ripening and seed preparation
Warm period	If no significant climatic dry season (e.g. summer)
Warmth + moisture	If some season is significantly dry (e.g. summer or monsoonal spring)

evolution towards DVMs that are more process based and explicitly consider dynamics while also taking into account key plant and soil processes such as photosynthesis, respiration and competition among a relatively few plant types. These models have been utilized in simulations across regional and global scales, including Arctic tundra and boreal ecosystems. However, their constituent PFTs historically had little detail in their representation. For example, Arctic tundra has commonly, and inappropriately, been represented as a C₃ grass in DVMs (Cramer *et al.*, 2001). One of the early DVMs was the LPJ (Lund–Potsdam–Jena) model, which represents global vegetation by only ten PFTs (Sitch *et al.*, 2003). However, the principle of the PFT approach was successful and led to the development of a range of different DVMs with more detailed representation of the vegetation by increasing numbers of PFTs (reviewed by Quillet *et al.*, 2010). While these coarse approaches may be practical and useful for certain (i.e. global) applications, a more detailed representation of the vegetation and the underlying processes is necessary to gain a deeper understanding of vegetation dynamics in high-latitude ecosystems. Chapin *et al.* (1996) recommended the use of Arctic- and boreal-specific PFTs in vegetation models, including evergreen trees, broad-leaved deciduous trees, deciduous conifers, deciduous shrubs, evergreen shrubs, sedges, grasses, forbs, *Sphagnum* moss, non-*Sphagnum* moss and lichens.

More recently, DVMs simulating tundra and boreal ecosystems have incorporated PFT groupings similar to those recommended by Chapin *et al.* (1996). An early model that simulated tundra plant dynamics based on a rich representation of 20 PFTs was ArcVeg (Epstein *et al.* 2000, 2001). Simulations using ArcVeg projected increases in deciduous shrub biomass and reductions in moss biomass under 3 °C of warming. These changes are very likely to alter the thermal regime of the soil, which has consequences for active layer processes and permafrost dynamics (Kade and Walker, 2008; Blok *et al.*, 2010; Lawrence and Swenson, 2011; Myers-Smith and Hik, 2013). The ArcVeg model also included PFT-specific grazing by Arctic herbivores, such as caribou and reindeer (Yu *et al.*, 2011). Interactions between tundra herbivores and an increasing abundance of forage shrubs could induce negative feedbacks on shrub encroachment, but also have implications for the lifestyles of native communities that subsist on reindeer or caribou (Kruse *et al.*, 2004; Forbes, 2013; Olofsson *et al.*, 2013). The Terrestrial Ecosystem Model with Dynamic Vegetation Model (TEM-DVM; Euskirchen *et al.*, 2009) included 39 PFTs across high-latitude vegetation types, such as heath, shrub, tussock and wet sedge tundra, as well as ecotonal boreal forest. Simulations with TEM-DVM have also shown increases in deciduous shrub abundance in northern Alaska, which lead to a decrease in summer albedo and an increase in land surface heat absorption for this region (Euskirchen *et al.*, 2009). Research conducted using the Community Climate System Model (CCSM4), and using only two PFTs, found that because of the spatial distribution of blowing snow, deciduous shrubs may warm the soil relative to graminoid-dominated tundra, thereby increasing the vulnerability of permafrost and stored carbon to thawing conditions (Lawrence and Swenson, 2011). Taken together, these results demonstrate how PFT dynamics in Arctic tundra (grass vs. deciduous shrubs) through important interactions with snow and snow cover can impact ecosystem structure and function in DVMs.

Numerous other DVMs are being applied to high-latitude systems (Table 3). A suite of these models define bioclimatic vegetation types and simulate the changing spatial patterns of vegetation (Rupp *et al.*, 2001; Kaplan *et al.*, 2003; Reich *et al.*, 2014). Kaplan *et al.* (2003) developed the BIOME4 model to examine high-latitude vegetation patterns and shifts in space and time by simulating the equilibrium distribution of Arctic tundra and boreal PFTs. One use of the model has been to compare simulated vegetation patterns in a given climate with observed paleo-vegetation. Simulations for the mid-Holocene reproduced northward forest expansion in western and central Siberia, in contrast to a stable forest limit in Beringia (Kaplan *et al.*, 2003). The Alaska Frame-Based Ecosystem Code (ALFRESCO) is a model that incorporates shifts among high-latitude ecosystem types over time, and it has been used to show long time lags associated with climate warming and tree-line advance in northern Alaska (Rupp *et al.*, 2001). More recently, the model has been applied to simulate boreal fire regimes (Rupp *et al.*, 2007; Johnstone *et al.*, 2011), and in particular how changes in fire regimes may influence animal habitat in western Alaska (Joly *et al.*, 2012). Another type of model commonly used is the individual-based gap dynamics model (e.g. Lischke *et al.*, 2007; Wolf *et al.*, 2008). Wolf *et al.* (2008) detailed a complex array of responses of vegetation in the Barents Region to future climate change using a version of the individual-based model LPJ-GUESS modified to include dynamics of tundra PFTs. These simulations show an advancement of treeline by 2100 that results in a decrease in tundra shrublands, and an expansion of tundra in the far north, replacing areas of barren ground. Another study using a version of LPJ-GUESS with additional tundra PFTs (Zhang *et al.*, 2013) projected a northward advance of the forest–tundra boundary, an expansion of shrub tundra and a shift from deciduous to evergreen boreal forest over northern Eurasia by 2080. Overall, the results from these simulations of vegetation pattern and migration indicate potentially significant changes in the distribution of Arctic and boreal vegetation types and ecosystem function in a warming climate, although the timing and spatial details of these shifts may differ depending on the model.

Recognizing the large carbon stocks and potential methane emissions associated with high-latitude peatlands, DVMs have recently begun incorporating peatland PFTs, as well as methane and related hydrological dynamics. Wania *et al.* (2009) incorporated PFTs pertaining to northern peatlands into the model LPJ-WHy, including flood-tolerant graminoids (e.g. *Carex* spp., *Eriophorum* spp., *Juncus* spp. and *Typha* spp.) and *Sphagnum* mosses. The inclusion of flood-tolerant graminoids in peatland dynamic vegetation models is important, since these plants possess aerenchyma, or gas-filled root, stem and leaf tissue, which facilitates the avoidance of anoxia. Aerenchyma also serves to transport methane and carbon dioxide from the soil to the atmosphere, an important but poorly understood process in tundra ecosystems (Kutzbach *et al.*, 2004). In a version of LPJ-WHy including these northern peatland PFTs and methane dynamics, the model was generally in good agreement with field data, although additional PFTs representing the differences in plant community composition between bogs and fens (and their underlying hydrological differences), as well as the inclusion of dwarf shrubs, may help to improve model performance (Wania *et al.*, 2010).

TABLE 3 Representation of plant functional types in Arctic and boreal ecosystems by dynamic vegetation models

Model	Plant functional types	Sources
ALFRESCO ArcVeg	Upland tundra, deciduous forest, white spruce, black spruce Moss, lichen, forb, tussock sedge, non-tussock sedge, grass, prostrate deciduous and evergreen shrub, dwarf deciduous and evergreen shrub, tall shrub, deciduous tree, evergreen tree	Rupp <i>et al.</i> (2007); Johnstone <i>et al.</i> (2011) Epstein <i>et al.</i> (2000, 2001)
BIOME4	Cold shrub, cold graminoid or forb, cushion forb, cold deciduous tree, cold needle-leaved evergreen tree	Kaplan <i>et al.</i> (2003)
CLM4-5*	Boreal needle-leaved evergreen tree, boreal needle-leaved deciduous tree, boreal broad-leaved deciduous tree, boreal broad-leaved deciduous shrub, C ₃ Arctic grass	Oleson <i>et al.</i> (2013)
CLM4Me [†]	Boreal needle-leaved evergreen tree, boreal needle-leaved deciduous tree, boreal broad-leaved deciduous tree, boreal broad-leaved deciduous shrub, C ₃ Arctic grass	Riley <i>et al.</i> (2011); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013)
CTEM	Needle-leaved evergreen tree, needle-leaved deciduous tree, broad-leaved cold deciduous tree, broad-leaved drought deciduous tree, C ₃ grass, C ₄ grass	Wang <i>et al.</i> (2006)
DigiBog	No specific PFTs; PFTs inferred from water-table depth and model different litter types	Baird <i>et al.</i> (2012); Morris <i>et al.</i> (2012)
DLEM	Tundra, boreal broad-leaved deciduous forest, boreal needle-leaved evergreen forest, deciduous shrub, evergreen shrub, C ₃ grass, seasonal herbaceous wetland, seasonal woody wetland, permanent herbaceous wetland, permanent woody wetland	Tian <i>et al.</i> (2010); Xu and Tian (2012); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013)
FAREAST GENESIS-IBIS HPM [‡]	Boreal forest, individual tree species, gap dynamics Tundra, desert, evergreen forest, deciduous forest, mixed forest Grass, minerotrophic forb, minerotrophic sedge, minerotrophic shrub, ombrotrophic forb, ombrotrophic sedge, ombrotrophic shrub, brown moss, hollow <i>Sphagnum</i> , hummock <i>Sphagnum</i> , feathermoss	Lutz <i>et al.</i> (2013); Shuman <i>et al.</i> (2013) Foley <i>et al.</i> (1998) Frolking <i>et al.</i> (2010)
IAP-RAS [†]	Bogs/mires, swamps, heaths/moorlands, tundra	Mokhov <i>et al.</i> (2007); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013)
LPJ-Bern [†]	Flood-tolerant graminoids, <i>Sphagnum</i> mosses, peatland	Spahni <i>et al.</i> (2011); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013)
LPJ-DGVM and LPJ-GUESS, LPJ-WSL	Boreal needle-leaved evergreen, boreal needle-leaved summergreen, boreal broad-leaved summergreen, tall shrub tundra, short shrub tundra, open ground tundra, wetland graminoid tundra, erect dwarf shrub tundra, prostrate dwarf shrub tundra	Sitch <i>et al.</i> (2003); Wolf <i>et al.</i> (2008); Hodson <i>et al.</i> (2011); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013); Zhang <i>et al.</i> (2013)
LPJ-WhyMe [†] MC1	<i>Sphagnum</i> mosses, and other upland PFTs based on water table Tundra, boreal coniferous forest, C ₃ grassland, taiga, boreal larch forest	Wania <i>et al.</i> (2009, 2010, 2013); Melton <i>et al.</i> (2013) Bachelet <i>et al.</i> (2001)
NASA-CASA NCAR LSM [§]	Tundra, high-latitude forest, boreal coniferous forest Cool needle-leaved evergreen tree, cool broad-leaved deciduous tree, cool mixed needle-leaved evergreen tree and broad-leaved deciduous tree, cool grassland, cool crop	Potter and Klooster (1999) Oleson and Bonan (2000)
ORCHIDEE [¶]	Boreal needle-leaved evergreen trees, boreal broad-leaved summergreen trees, boreal needle-leaved summergreen trees	Krinner <i>et al.</i> (2005); Ringeval <i>et al.</i> (2010); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013)
PDM SDGVM	Bog, fen Needle-leaved deciduous trees, broad-leaved deciduous trees, needle-leaved evergreen trees, C ₃ grass, C ₄ grass	Frolking <i>et al.</i> (2001) Hopcroft <i>et al.</i> (2011); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013)
TEM-DGVM	Parameterizations for community types including white spruce forest, heath tundra, shrub tundra, tussock tundra, and wet sedge tundra. PFTs are parameterized differently, depending on the community type in which they are found, and include: white spruce trees, dwarf birch shrubs, willow shrubs, other deciduous shrubs, evergreen shrubs, sedges, grasses, forbs, <i>Sphagnum</i> mosses, feathermosses, lichens	Euskirchen <i>et al.</i> (2009, 2014)
TreeMig	Individual-based model with a focus on boreal tree species. Tundra is simulated simply as grasses and shrubs	Lischke <i>et al.</i> (2007)
VEGAS VISIT/Sim-CYCLE	Broad-leaved tree, needle-leaved tree, cold grass Tussock tundra, tundra, boreal evergreen forest, boreal deciduous needle-leaved forest	Zeng <i>et al.</i> (2005) Ito and Inatomi (2012); Ito and Oikawa (2002)
UVic-ESCM	Broad-leaved trees, needle-leaved trees, C ₃ grass, C ₄ grass, shrub	Avis <i>et al.</i> (2011); Melton <i>et al.</i> (2013); Wania <i>et al.</i> (2013)

*Latest version of the CLM.

[†]For methane emission from wetlands.[‡]For peatland.[§]Boreal forest only.[¶]The same as LPJ.

Other DVMs include peatland PFTs to better represent processes leading to methane production in global wetlands, yet the differences in simulated methane emissions among ten

models included in the WETCHIMP intercomparison were substantial (Melton *et al.*, 2013). These differences in methane flux estimates arise in part because of variation in model

complexities, spatial scale of intended use, areal extent of wetlands and a variable representation of wetland PFTs among the various models. In addition, a review on the inclusion of mosses in high-latitude process-based models of boreal peatlands and Arctic tundra found a need for reducing uncertainty in moss community response to disturbance, controls on moss population viability, and moss–vascular plant competition under changing resource availability as a means toward more accurate representation of mosses in models (Turetsky *et al.*, 2012). Given that non-frozen peatlands with boreal characteristics (e.g. tree cover and a large percentage of mosses) are expected to expand further north into the Arctic tundra as temperatures rise, it is important to represent this key PFT accurately in ecosystem and dynamic vegetation models. In ecosystems dominated by mosses, a single moss PFT may be inadequate, as there are important differences in morphology, physiology and potential feedbacks from the ecosystem between *Sphagnum* mosses in hollows vs. hummocks, and between brown and feathermosses. The Holocene Peatland Model (Frolking *et al.*, 2010) determines vegetation composition and net primary productivity (NPP) based on peat depth and water-table depth. The model includes 12 PFTs, seven of which are vascular plants and five of which represent different non-vascular plants. The five non-vascular PFTs are defined by location (hollow, hummock and lawn) and major plant form (brown moss, *Sphagnum* and feathermoss), and are parameterized by their productivities at an optimum water-table depth, peat depth and decomposition characteristics. Each PFT, including the non-vascular PFTs as parameterized, contributed uniquely to total peat NPP over the 8500-year simulations (Frolking *et al.*, 2010).

These studies have reinforced the importance of including appropriate PFTs for these given ecosystems into DVMs. While the absence or presence of a particular PFT is important, it is also true that PFTs must be appropriately parameterized. In their attempts to improve the representation of near-surface permafrost in CCSM4, Lawrence *et al.* (2012) emphasized that present-day ESMs do not capture the influence of specific PFTs on the interplay of snow, soil thaw and growing season length that govern the carbon dynamics of high latitude, and therefore these models tend to overestimate the degree of permafrost thaw and degradation. A solution to this was to link PFTs more closely to soil organic matter, thermal conductivity and soil water content, and more faithfully represent the insulating properties of this structural component for Arctic and boreal ecosystems (Lawrence and Slater, 2008; Lawrence *et al.*, 2008). In turn, Jiang *et al.* (2012) showed that the parameters that control plant CO₂ uptake and light-use efficiency in LPJ-DGVM were as important as climate in influencing the distribution of both woody and herbaceous PFTs. Many of these impacts were greatest in areas of the Arctic where a northward expansion of grasses and treeline migration were observed with increasing temperature. Likewise, Euskirchen *et al.* (2014) recently reported that including PFT-specific timing of leaf initiation (i.e. phenology) into a DVM influences both the structure and function of Arctic and boreal ecosystems, and resulted in a better agreement of the model with field data (Fig. 2). This work clearly demonstrates the importance of adequately assigning traits, including temporal traits, to PFTs, and argues for an expanded effort to collect data in high-latitude ecosystems for critical parameters across a range of PFTs.

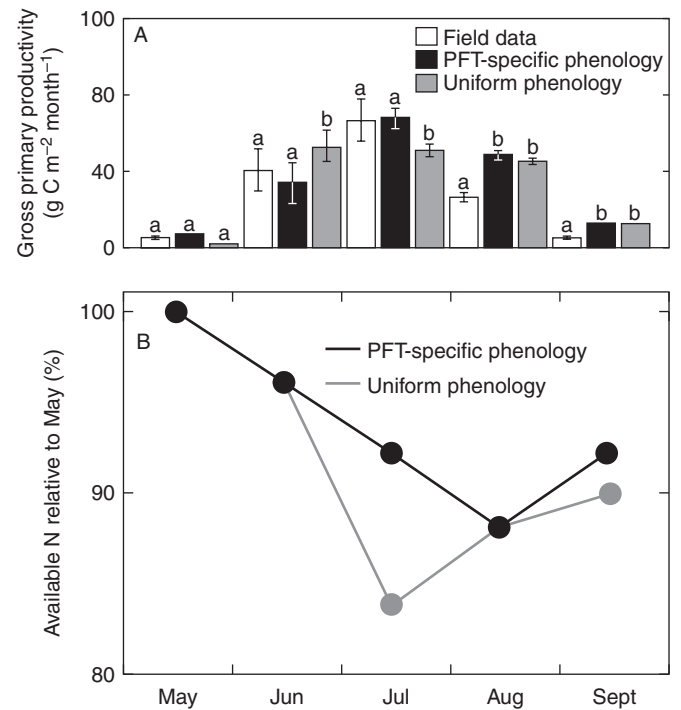


FIG. 2. (A) Comparison between gross primary productivity ($\text{g C m}^{-2} \text{ month}^{-1}$) calculated based on eddy co-variance tower measurements in tussock tundra at the Imnavait Watershed in northern Alaska (Euskirchen *et al.*, 2012) and model-simulated gross primary productivity for a version of TEM-DVM with the leaf phenology algorithm where leaf onset occurs individually for a PFT (modified model) and the version of the model where all the PFTs in the tussock tundra leaf out at the same time (previous model version). Letters above the bars indicate significant differences for a given month and ecosystem type, based on a Bonferroni multiple range test. The modified model shows better agreement with the field data than the previous version of the model. In particular, the modified model captures the timing of peak carbon uptake in July. (B) This dynamic appears to be related largely to the available nitrogen (N) in a given month, relative to the month of May. While the available N generally decreased from May to August in both the modified and previous version of the model, in the previous version the available N was consistently lower in July than in the modified model. This was due to the overall later leaf out in the modified version of the model, indicating that the plants used less N earlier from the available N pool early in the growing season, with more to use later in the growing season, thereby permitting gross primary productivity to peak in July. Leaf senescence in the autumn occurs at the same time for all PFTs in both versions of the model due to lack of field data for parameterization, which may explain the differences between the field data and the model in August and September.

EMERGING PARADIGMS FOR VEGETATION MODELLING

The DVMs developed for Arctic and boreal ecosystems have provided important insights into vegetation dynamics in current and future climates. They indicated the drivers of shrub encroachment (Epstein *et al.*, 2000; Euskirchen *et al.*, 2009); the critical role of moss with respect to thermal dynamics of permafrost-dominated ecosystems (Frolking *et al.*, 2010); the contribution of flood-tolerant graminoids to methane fluxes from Arctic and boreal soils (Wania *et al.*, 2009); and how changes in vegetation composition can affect carbon source–sink relationships in interaction with snow cover and permafrost thaw (Lawrence *et al.*, 2012). Despite the insights gained, the current models have several key shortcomings. The PFTs in the previously

described models are distinguished based on categorical traits, and parameterized using constant trait values, thus assuming a strong, invariable link between form and function in current and future climates. Although conceptually appealing, the validity of this assumption should be carefully investigated and the consequences for modelling vegetation dynamics and ecosystem function quantified.

Morphological and physiological traits related to carbon, water and nutrient cycling have been shown to vary strongly within PFTs at a global scale (van Bodegom *et al.*, 2012). Based on recent aggregation of trait data (Kattge *et al.*, 2011), substantial variation in key traits within PFTs can also be demonstrated for regional applications (Fig. 3). To obtain credible DVMS that reliably quantify vegetation dynamics and biogeochemical cycling in the context of future climate projections, accounting for this variability in physiological traits (e.g. as related to photosynthesis, nutrient resorption, etc.) may be essential. For instance, Aerts *et al.* (2012) showed strong responses in leaf litter nutrient concentrations within PFTs across various global change treatments. These changes, and how they affect litter decomposition, as well as the extent to which relationships between litter chemistry and decomposition are decoupled in a future climate (Aerts *et al.*, 2012), need to be considered in DVMS. Similarly, various studies have shown highly species-specific impacts on methane emissions, also within Arctic and boreal PFTs (Ström and Christensen, 2007; Koelbener *et al.*, 2010). Thus, to obtain robust estimates of regional methane emissions, which is an important target of these vegetation models (Melton *et al.*, 2013), quantifying within-PFT differences may be crucial. Even treeline advancement has been shown to be highly variable within PFTs (Elmendorf *et al.*, 2012a), and for this purpose inclusion of variability within morphological and physiological traits may provide new quantitative insights.

Current PFT classifications (and model implementations) often neglect root traits and instead focus on above-ground properties and processes, as evidenced by common PFT terminology (e.g. evergreen, deciduous and C₃/C₄ grasses). However, the interaction of plant roots with the surrounding soil environment

has been shown to exert important controls over the effect of changing climatic conditions on Arctic and boreal ecosystems (Hartley *et al.*, 2012). A recent review indicates that mean below-ground biomass of PFTs in Arctic tundra can be between two and seven times as much as above-ground biomass. Root traits including morphology, chemistry, porosity, exudation rates, depth distribution and mycorrhizal colonization can differ strongly within the same life form (Pohl *et al.*, 2011) and can affect ecosystem carbon and nutrient cycling (Chapin *et al.*, 1993; Nowinski *et al.*, 2008; Keuper *et al.*, 2012) and methane emissions (Ström *et al.*, 2012). The poor representation of root traits in PFT classifications and their parameterization stems directly from the difficulty of measuring root properties, especially in cold, water-saturated high-latitude ecosystems. A potential near-term solution to overcoming a lack of information on root traits across PFTs would be to employ an economics spectrum perspective to vegetation dynamics (Freschet *et al.*, 2010). Such a view has the benefit that co-variation among above- and below-ground plant traits (e.g. Craine *et al.*, 2003; Freschet *et al.*, 2010; McCormack *et al.*, 2012) may allow estimation of root traits for PFTs where very few data are available.

Trait variability above- and below-ground can be incorporated into DVMS in multiple ways. One approach would be to vary parameters within PFTs as a function of environmental variables. Such an approach has the rationale that community (or PFT) mean trait values are selected by environmental conditions, thus causing trait convergence. This selection by the environment is expressed in empirical trait–environment relationships, which have shown globally consistent patterns relating leaf functional traits to climate (Wright *et al.*, 2005), soil fertility (Ordoñez *et al.*, 2009) or combinations thereof (e.g. Ordoñez *et al.*, 2010; van Ommen Kloeke *et al.*, 2012). Incorporation of empirical trait–environment relationships into the JSBACH DGVM, which is part of the Max Planck Institute Earth system model (MPI-ESM), indicated major consequences of trait variability on vegetation and carbon dynamics for the current climate (Verheijen *et al.*, 2013).

Similar relationships may be derived specifically, or otherwise modified from existing correlations, for northern high-latitude ecosystems within DVMS. Environmental drivers known to be important to Arctic and boreal PFTs, including the number of frost days, but also soil moisture and nutrient availability, are likely to be essential for refining mechanistic-based models of Arctic ecosystems and for linking biogeochemical cycling models to vegetation dynamics models in an integrated, coupled land–climate model framework for both regional and global scales. Such trait responses could be inferred, for example, from observations across gradients of permafrost degradation (Schuur *et al.*, 2009). A working hypothesis is that permafrost degradation causes a change in water and nitrogen availability and distribution that will drive changes in trait expression and PFT distribution across the landscape. The data needed to test this hypothesis and develop the functional relationships for modelling include seasonal variation in active layer nitrogen availability, plant–soil feedbacks that alter carbon–nitrogen cycling and nitrogen availability, plant utilization of available nitrogen (including seasonal dynamics, root distribution and nitrogen fixation) and root distribution of plants in relation to water. A combination of empirical data and insights generated via a model of carbon–nitrogen interactions (Xu

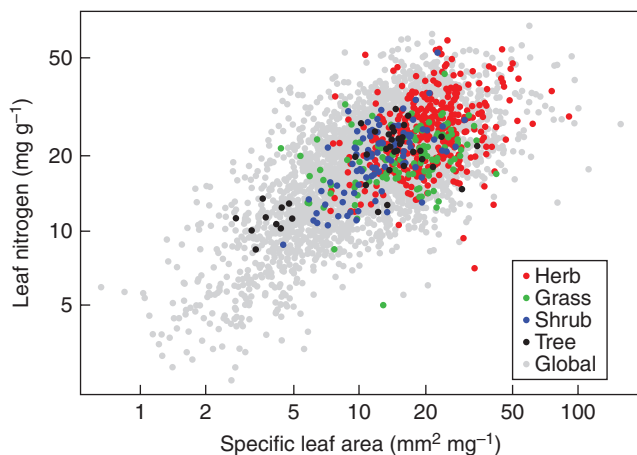


FIG. 3. Variation in specific leaf area and leaf nitrogen concentration per unit dry mass for boreal herbs, grasses, shrubs and trees. The points in grey (global) are for species from a larger, worldwide set of observations. The data for herbs, grasses, shrubs and trees present species mean trait values for 599 plant species and 4483 species worldwide from the TRY database of plant traits (Kattge *et al.*, 2011).

Note that the *x*- and *y*-axis are both plotted on a log scale.

et al., 2012) could help clarify and establish the importance of variation in nitrogen acquisition and allocation strategies within and between PFTs in areas of thawing permafrost.

Another approach is to incorporate trait variability based on trade-offs and evolutionary rules to determine the survival of trait combinations within a given PFT for a suite of environmental conditions (Kleidon and Mooney, 2000; Scheiter and Higgins, 2009). Information on trait trade-offs, including co-varying above- and below-ground traits (Freschet *et al.*, 2010; Sloan *et al.*, 2013), and on trait impacts on carbon fluxes in high latitudes (Cornelissen *et al.*, 2007; Freschet *et al.*, 2011) is already available. With this type of information, the first semi-quantitative models based on eco-evolutionary principles for northern high-latitude ecosystems could be constructed. For this approach to operate quantitatively, however, a complete quantitative understanding of allometric relationships for Arctic and boreal PFTs would be required (i.e. to predict differences in above- and below-ground biomass). Moreover, an expanded understanding of the carbon or energy costs associated with high-latitude adaptations (e.g. cold tolerance) would be necessary. Such insights are beginning to emerge (Lenz *et al.*, 2013). A comprehensive understanding of how different trade-offs relate to different PFT architectures (e.g. between tussock and non-tussock graminoid growth forms) would provide additional insights to incorporate into PFTs. While such information is partially available, it has not yet been compiled in an eco-evolutionary-based optimality approach. Finally, a more radical approach would be to abandon PFTs altogether and apply optimality principles (Pavlick *et al.*, 2013) or empirical relationships to predict trait prevalence and vegetation distributions (Reu *et al.*, 2011a, b). Neither of these approaches, however, has been implemented in Arctic and boreal DVMs. Nonetheless, it seems feasible to incorporate variable-trait approaches for the modelling of vegetation dynamics, and carbon and nutrient cycling in northern high-latitude ecosystems.

VALIDATION AND BENCHMARKING OF PREDICTED VEGETATION PATTERNS

While multiple efforts are underway to enhance the PFT representation within local, regional and global models, data on the spatial extent of vegetation types are required for benchmarking and validation purposes (Sitch *et al.*, 2003; Kelley *et al.*, 2013). Numerous efforts over the past decades to document the geographic patterns of Arctic tundra vegetation, at scales ranging from the plot to circumpolar, have proven extremely useful benchmarks for predicting changes in Arctic tundra PFTs (Kaplan and New, 2006). Probably the most comprehensive effort over the broadest spatial extent was the development of the Circumpolar Arctic Vegetation Map (CAVM Team, 2003). The CAVM, with polygons mapped at the 1:7.5 million scale, contains five broad categories sub-divided into a total of 15 vegetation mapping units, with the PFT concept driving the development of these distinct vegetation sub-units. The five physiognomic categories were barrens, graminoid tundra, prostrate shrub tundra, erect shrub tundra and wetlands, distinguished by their dominant PFTs. The sub-divisions of each of these broader categories were also determined by the relative abundances of the PFTs. For example, graminoid tundra was

divided into four sub-categories that included communities dominated by rushes, grasses, tussock sedges and non-tussock sedges.

Some Arctic tundra vegetation maps have been developed at finer resolutions (e.g. regional–continental scale). Muller *et al.* (1999) used Landsat Multi-Spectral Scanner imagery to develop a map of Arctic tundra vegetation types for northern Alaska at a resolution of 100 m. The vegetation classes were defined by the dominant PFTs and include moist graminoid/prostrate shrub tundra, moist tussock graminoid/dwarf shrub tundra, wet graminoid tundra, dry prostrate shrub tundra and moist dwarf shrub/tussock graminoid tundra. For northern Canada, Gould *et al.* (2003) developed a tundra vegetation map at a finer scale (1:4 000 000) than the CAVM using a variety of data sources, including the Advanced Very High Resolution Radiometer (AVHRR) colour infrared image basemap. The vegetation map produced in this effort included 17 vegetation types, and there was also an aggregated map of the biogeography of 11 PFTs. These PFTs included lichens/bryophytes, cushion forbs, three graminoid types and six shrub types. Therefore, both the CAVM and these regional-scale PFT maps provide some excellent spatial, and eventually temporal, benchmarks for assessing PFT dynamics. Similar efforts are underway to map vegetated wetlands throughout Arctic and boreal regions of Alaska, although the current location, types and extents of wetlands (e.g. fens and bogs) in high-latitude ecosystems are uncertain (Whitcomb *et al.*, 2009).

As the examples just described suggest, a variety of remote-sensing products are available for benchmarking model simulations. The extensive coverage in space and time by satellite and airborne imaging provides an unparalleled set of Earth observational data for such purposes. Airborne *in situ* measurements can also provide complementary value-added data. However, the available data products from the presently operating satellite sensors are not always readily usable for model benchmarking and validation, since DVMs often track variables not directly measured by remote sensors (e.g. net ecosystem exchange and active layer depth). Hence, additional processing of the directly measured remote-sensing data is needed to convert spectral information into key model variables, such as gross or net primary productivity. Additionally, several technical issues pose significant challenges to the production of remote-sensing data sets useful for comparison with model results, including resolution mismatches between sensors and models, orbital constraints on timing and frequency of observations, difficulties with atmospheric corrections, and obscuring of surface properties by clouds and snow cover. Some of these issues are more prominent in high-latitude ecosystems and would potentially increase uncertainties when using remote sensing for benchmarking and validation of high-latitude DVMs.

In addition to using existing spatially explicit maps for model benchmarking and validation, several networks across the Arctic and boreal region are also poised to provide data for model parameterization and initialization. Investigators at a number of co-ordinated networks are collecting site-specific data on plant species composition, leaf area index and biomass of various PFTs. One of the most comprehensive, extensive and long-running networks is the International Tundra Experiment (ITEX; Walker *et al.*, 2006; Elmendorf *et al.*, 2012a, b). The ITEX is a collection of sites in Arctic and alpine tundra with a

common warming experiment (using passive-warming open-top chambers) and a consistent sampling protocol (largely point-frame data collection) across locations. Thus, for more than two dozen sites throughout the Arctic, data exist on the absolute and relative abundances of various tundra PFTs, obtained through non-destructive sampling. As an example, Oberbauer *et al.* (2013) used 12 sites in the ITEX network to examine the phenological responses of graminoids, forbs, and deciduous and evergreen shrubs to interannual climate variability. Over the past decade or more, a number of research projects have provided the opportunity for the development of two tundra-wide transects: the North American and the Eurasian Arctic transects (Walker *et al.*, 2012). Each of these two transects spanned the full latitudinal gradient of the Arctic across all five tundra sub-zones (CAVM Team, 2003), and there are comprehensive and consistent data on floristic characteristics, leaf area index and above-ground biomass across 13 sites (Alaska, Canada and Siberia) for six PFTs, i.e. mosses, lichens, graminoids, forbs, evergreen shrubs and deciduous shrubs (Walker *et al.*, 2012). Finally, data on PFTs have been collected from a number of sites, some of which also have ITEX installations, that could be used for additional benchmarking locations, including (but not limited to) Toolik Lake Long-Term Ecological Research station (Low Arctic Alaska, USA), Barrow Environmental Observatory (High Arctic Alaska, USA), Devon Island, Alexandria Fjord (Canadian Arctic), Zackenberg Ecological Research Operations (north-east Greenland), Abisko Scientific Research Station (Sweden), Ny-Ålesund (Svalbard) and Cherskii Field Station (north-east Siberia, Russia).

With regard to validation of modelled projections of changes in tundra PFTs, the aforementioned ITEX network may be the most useful set of spatially explicit information. Data from ITEX locations, with passive warming experiments of different durations, have been used to compare with model results. In fact, output of vegetation dynamics from the ArcVeg model (Epstein *et al.*, 2004) was compared with observed vegetation changes from a synthesis of ITEX sites (Walker *et al.*, 2006). In a recent study, Elmendorf *et al.* (2012b) synthesized results from 61 experimental warming studies with durations of up to 20 years and found that shrubs increased in response to warming essentially where average temperatures were already high, whereas graminoids increased with warming in the colder sites, indicating regional differences in PFT responses to warming. These kinds of results will probably be most useful in validating simulation model output of PFT dynamics. In addition to the passive warming treatments of the ITEX network, other sites scattered throughout the Arctic have hosted other passive as well as active warming experiments that could be used for PFT modelling validation (e.g. Buizer *et al.*, 2012; Henry *et al.*, 2012; Kaarlejarvi *et al.*, 2012; Zamin and Grogan, 2012; Campioli *et al.*, 2013; Sharp *et al.*, 2013; Sistla *et al.*, 2013). Several experimental studies are currently underway, including soil warming and water-table manipulations, near the Bonanza Creek Experimental Forest in interior Alaska where an emphasis is being placed on understanding boreal forest dynamics in a changing climate (Turetsky *et al.*, 2008; Kane *et al.*, 2013). These studies offer additional insights into the responses of different PFTs to environmental change (i.e. disturbance regimes), and the use of those data for model parameterization and validation.

RECOMMENDATIONS AND CONCLUDING REMARKS

Plant functional types have offered both the biologist and the modeller a tractable scheme to represent plant diversity and associated function in models of the terrestrial biosphere. Although alternatives or refinements have been suggested (Pavlick *et al.*, 2013; Scheiter *et al.*, 2013) and may emerge as new avenues for model improvement, the PFT concept is currently well integrated into DVMs and thus is likely to persist as an approach to reduce biological complexity in models for the foreseeable future. As the community continues to rely on PFTs to represent plant species and their dynamics in models, several advancements are needed, including (1) PFT classification, especially related to the integration of remote sensing, mapping, and validation of current and projected patterns of vegetation distribution; (2) inclusion of appropriate PFTs in regional models, paying close attention to trait-based characteristics that influence biogeochemical and biophysical functioning of ecosystems; (3) trait identification, database compilation and dynamic parameterization of PFTs for above- and below-ground properties and processes; and (4) data development for model benchmarking and validation. In addition, we advocate for model development to improve the representation of competition among PFTs, successional dynamics and disturbance.

Several researchers have recently raised important questions about the need to better integrate PFT classification activities with vegetation mapping and model validation efforts using remote-sensing and ground-truthing approaches. Sun and Liang (2007) and Sun *et al.* (2008) emphasized that because of species diversity and variation in spectral characteristics, accurate monitoring and mapping of PFTs is a difficult task and, as a result, no satisfactory methodology exists for the extraction of PFT classifications from satellite observations. This often leads to a disconnection between field observations and model projections. A possible solution to this dilemma may be classification of PFTs consistent with satellite sensors and their derived products. Poulter *et al.* (2011) recognized this and showed how major sources of uncertainty in a widely used DVM (LPJmL) could be addressed by cross-walking or reclassifying land cover types to broader PFT categories based on land cover information for three satellite sensors (EOS-MODIS, SPOT4-VEGETATION and ENVISAT-MERIS). Additional efforts that facilitate a close collaboration among modellers, plant geographers and those who acquire and process remote-sensing data sets should be encouraged. An excellent illustration of this is reflected in the recent concept of ‘optical type’ as a means to link structural, physiological and phenological traits with optical properties of PFTs (Ustin and Gamon, 2010). Assessing the connections among these traits and evaluating their utility in DVMs would benefit from the further involvement of plant ecologists and modellers who could bring additional insights and perspectives to the analysis of such a potentially novel approach.

Despite the utility of remote sensing to the identification and mapping of PFTs at regional to global scales, there are limits to this approach. Satellite- and aircraft-based imaging tends to neglect important PFTs, especially those encompassing non-vascular species. This occurs despite knowledge that non-vascular plant types and communities play a vital role in

ecosystem function, especially in northern latitudes. For example, Turetsky *et al.* (2012) emphasized the important role that mosses play in the structure and function of Arctic and boreal ecosystems, a conclusion that was similarly echoed through model evaluation (Lawrence and Slater, 2008; Lawrence *et al.*, 2008). Engstrom *et al.* (2006) uniquely and appropriately added non-vascular vegetation (mosses) to the BIOME-BGC model to simulate evapotranspiration in Arctic coastal plain systems. Mosses and lichens have also been incorporated as PFTs into the Terrestrial Ecosystem Model (TEM) and parameterized using site-specific knowledge (Euskirchen *et al.*, 2009); thus this model and a few others (e.g. ArcVeg; Epstein *et al.*, 2000) can simulate the functional role of these PFTs for permafrost stability and grazing (Yu *et al.*, 2009, 2011). Lichens in particular are crucial for understanding vegetation–herbivore interactions, as they are a main source of winter nutrition for grazing animals in tundra (Thompson and McCourt, 1981; Johnstone *et al.*, 2002). However, while models have begun to simulate lichen abundance and other forage species important for grazing animals, the feedback on how grazing controls plant growth and PFT abundance has not been taken into account by models (Zamin and Grogan, 2013). Furthermore, when short-stature PFTs such as mosses and lichens are incorporated into models, it is important to incorporate competition among PFTs due to light availability since increasing abundance of taller, vascular plants may decrease the amount of light available to mosses and lichens, thereby causing them to decline (Cornelissen *et al.*, 2001). Global data sets such as the TRY initiative (Kattge *et al.*, 2011) currently contain little information on non-vascular cryptogams (i.e. bryophytes and lichens), despite their diversity in species, functions and ecosystem effects. This deficiency must be overcome and is probably one that also needs to be addressed alongside challenges of identifying non-vascular PFTs via remote sensing.

The geographical distribution of plants and hence spatial patterns of PFTs is determined by plant–plant competition, mediated by climate, soils and various forms of disturbance including fire, permafrost thaw, insects and disease. In a recent review, Scheiter *et al.* (2013) outlined a series of deficiencies in DVMs and how those could be addressed assuming that next-generation models adopted principles from community assembly and coexistence theories used in ecology. Several of those deficiencies focused on reproduction, competition and the consequences of resource availability (e.g. water or nutrients) on the distribution of vegetation based on how plants with different trait combinations perform under a particular environmental condition (e.g. temperature, light and CO₂) and disturbance regimes (e.g. fire and windthrow). For the Arctic and boreal regions, competition, successional dynamics and disturbance are important considerations for the trajectories of ecosystems in a changing climate, yet DVMs are just now beginning to capture these interactions in high-latitude ecosystems and elsewhere (Haverd *et al.*, 2013; Kantzas *et al.*, 2013). Furthermore, understanding resource use and acquisition across broad categories of plant species remains a key challenge in modelling competition among PFTs. For example, to model competition for soil water among PFTs, information on rooting depth and root mass in a given layer of soil is important, but little information is available on rooting characteristics for high-latitude PFTs. Changes in PFTs following disturbance and subsequent

succession during recovery may also be difficult to capture, particularly for Arctic and boreal vegetation transitions under conditions of, for example, fire and thermokarst. While we have a general understanding of the changes in vegetation types likely to occur, we often do not know the relative abundance of PFTs within recently disturbed ecosystems, and indeed some of these may be unique, ‘no-analogue’ communities (e.g. Williams and Jackson, 2007). Thus it appears that more information is needed on traits that determine the competitive behaviour of PFTs, and on how these ecosystems develop during succession following a disturbance, if we are to make reliable projections of carbon, nutrient, water and energy budgets for high-latitude ecosystems.

Many of the deficiencies we have identified can only be resolved through the availability of regional and global data sets of plant characteristics (‘traits’) and trait-based strategies that can be used within the PFT framework. Fortunately, the last few years have seen an increase in trait identification, data compilation and inventories, and analyses of those data sets for (among other uses) parameterization of PFTs across a wide range of above- and, to a lesser extent, below-ground properties and processes. The TRY database is especially noteworthy in this regard as a global inventory of plant traits, many of which have application in the parameterization of PFTs (Kattge *et al.*, 2011). This initiative began as a modest effort, but has quickly grown into a data repository that currently contains almost 5 million trait entries for 80 000 of the world’s 300 000 plant species. The global trait database has been used in many ways, not only to assign traits to PFTs used in models (McMahon *et al.*, 2011), but also to develop hypotheses that might lead to a replacement of fixed PFT parameters with more continuous trait variables or spectra (Kattge *et al.*, 2011). Additional contributions to the TRY initiative from existing databases and new measurements are needed, however, to encompass the tremendous global diversity in traits for vascular and non-vascular plants. For example, TRY currently contains little information on non-vascular cryptogams (i.e. bryophytes and lichens), despite their diversity in species, functions and ecosystem effects. Root traits, in particular, are also largely missing from the database, with coarse measures of rooting depth being the primary below-ground variable; root distribution as a trait is available for only 0.05 % of the vascular plant species (Kattge *et al.*, 2011). This must be improved, as well as additional data collected and contributed on root traits, including a range of root structure and functional characteristics. One such attempt to compile and analyse existing root data from Arctic tundra ecosystems and to identify knowledge gaps that could be filled by future studies is already underway. An expanded set of traits and their availability for inclusion into models will greatly enhance the representation of biological processes, feedbacks and interactions in terrestrial ecosystems.

Recent observations and historical information suggest that high-latitude terrestrial ecosystems are experiencing rapid and unprecedented changes in climate (Hinzman *et al.*, 2013). Knowing how the structure and function of Arctic and boreal ecosystems will respond to persistent climatic change is a significant challenge, one in which vegetation plays a central, albeit uncertain, role. Models that incorporate the PFT concept can provide valuable insights into the emerging patterns of vegetation change in tundra and boreal forests, given known processes

of tree mortality, treeline migration and shrub expansion. However, DVMs require consistent evaluation based on knowledge provided by the plant biologist and others working with modellers to improve representation of critical processes. In this review, we have identified a few of those across diverse scientific disciplines of taxonomy, biology, biogeography, remote sensing, data management and modelling. Progress has been made in recent years to improve representation of vegetation dynamics and the inter-relationships among vegetation, biogeochemistry and feedbacks to climate. Much work remains and, given the sensitivity of high-latitude ecosystems to warming temperatures, steps should be taken to assemble expertise across many fields and conduct the collaborative research necessary to reduce uncertainties in DVMs and ultimately ESMs.

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