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Comparing assumptions and applications of dynamic vegetation models used in the Arctic-Boreal zone of Alaska and Canada

To cite this article: Elise Heffernan *et al* 2024 *Environ. Res. Lett.* **19** 093003

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RECEIVED
30 May 2024REVISED
10 July 2024ACCEPTED FOR PUBLICATION
22 July 2024PUBLISHED
7 August 2024

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Comparing assumptions and applications of dynamic vegetation
models used in the Arctic-Boreal zone of Alaska and CanadaElise Heffernan^{1,*} , Howard Epstein¹, T Declan McQuinn¹, Brendan M Rogers², Anna-Maria Virkkala²,
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E-mail: eh9hg@virginia.edu**Keywords:** dynamic vegetation model, Arctic-Boreal zone, ecosystem modeling**Abstract**

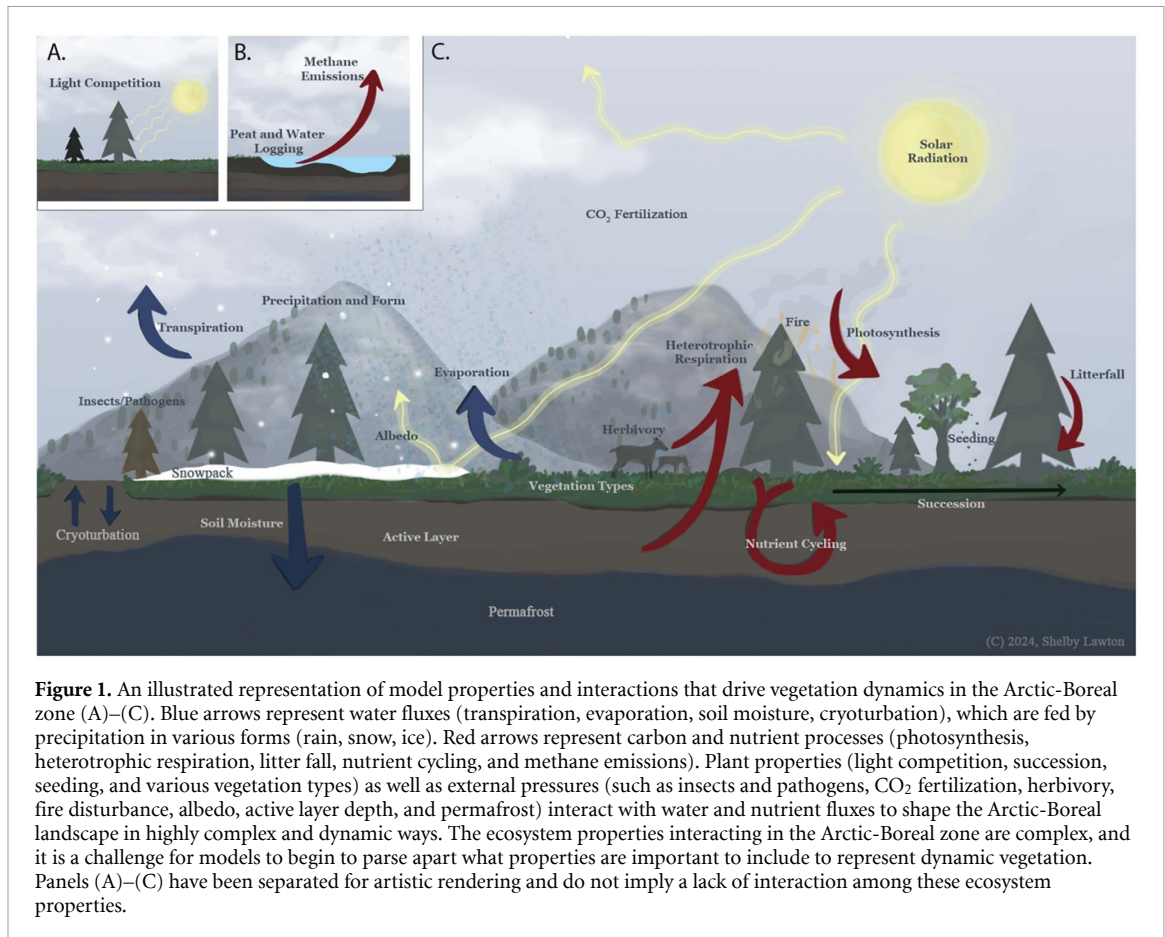
Modeling Arctic-Boreal vegetation is a challenging but important task, since this highly dynamic ecosystem is undergoing rapid and substantial environmental change. In this work, we synthesized information on 18 dynamic vegetation models (DVMs) that can be used to project vegetation structure, composition, and function in North American Arctic-Boreal ecosystems. We reviewed the ecosystem properties and scaling assumptions these models make, reviewed their applications from the scholarly literature, and conducted a survey of expert opinion to determine which processes are important but lacking in DVMs. We then grouped the models into four categories (specific intention models, forest species models, cohort models, and carbon tracking models) using cluster analysis to highlight similarities among the models. Our application review identified 48 papers that addressed vegetation dynamics either directly (22) or indirectly (26). The expert survey results indicated a large desire for increased representation of active layer depth and permafrost in future model development. Ultimately, this paper serves as a summary of DVM development and application in Arctic-Boreal environments and can be used as a guide for potential model users, thereby prioritizing options for model development.

1. Introduction

The Arctic-Boreal zone (ABZ) constitutes a range of highly dynamic ecosystems that are rapidly changing due to anthropogenic climate change (Fyfe *et al* 2013, Box *et al* 2019, Ballinger 2021). Warming is occurring at an accelerated rate as a consequence of Arctic amplification (Goosse *et al* 2018, Chylek *et al* 2022), in turn causing decreased spring snowpack (Callaghan *et al* 2011, Heijmans *et al* 2022), decreased albedo (Chapin *et al* 2005), permafrost thaw (Campbell *et al* 2021, Miner *et al* 2022), higher severity and frequency of fires (Timoney *et al* 2019, Cahoon *et al* 2022), increased available nitrogen (Salmon *et al* 2016), and changes to carbon cycling (Schuur *et al* 2022, Pedron *et al* 2023). These effects of warming influence vegetation dynamics, and in turn are impacted

by changing vegetation properties (figure 1). The ABZ spans boreal and tundra biomes, where these climate effects are manifesting in diverse vegetation shifts such as Arctic shrubification (Myers-Smith *et al* 2015, Maliniemi *et al* 2018, Rees *et al* 2020), altered treeline extent and density (Rees *et al* 2020, Dial *et al* 2024), decreased lichen abundance (Elmendorf *et al* 2012), and shifts in deciduous tree cover (Mack *et al* 2021, Massey *et al* 2023).

Cycles of succession and shifting vegetation are characteristic of the heterogeneous ABZ landscape, especially in the fire-adapted boreal forest (Rogers *et al* 2015). Connecting environmental processes to vegetation changes and subsequent interactions in the ABZ (figure 1) is critical to better predict vegetation dynamics in the region. However, because anthropogenic climate change has been altering



Earth's ecosystems for decades and is amplified in the Arctic (Previdi *et al* 2021, Rantanen *et al* 2022), a static representation of vegetation in the ABZ locks assumptions into a model simulation that may not be representative of either a pre-warming Arctic, nor of an 'adapted' Arctic (Loehle 2018). Thus, predictions of the Arctic-Boreal future must include vegetation that can respond to changing environmental properties.

With advances in computing power, ecosystem simulation models are now able to better represent their target systems. Dynamic vegetation models (DVMs) are a class of ecosystem simulation model making great advances due to increased availability of input data, as well as heightened model development and sophistication in simulating ecosystems (Fisher *et al* 2018a, 2018b, Bugmann and Seidl 2022). For this study, a DVM was defined as having the capability for terrestrial vegetation (be it plant species, functional type, cohort, community, or ecosystem type) to respond (via yearly growth, changing stem density, vegetation migration, and mortality, among others) to climate and other environmental factors. As a result, an area represented by a DVM must be capable of having its vegetation composition, its structure, and/or function fluctuate over time in response to changing conditions. A DVM can predict how vegetation competition (from intra- and interspecific to inter-community type) will respond

to environmental inputs and determine ecosystem-level changes. This broad suite of models can simulate a range of possibilities and highlight the largest uncertainties (Fisher *et al* 2018a, Krause *et al* 2019, Gädeke *et al* 2020, Argles *et al* 2022).

DVMs can require substantial parameterization, as they often have fine vegetation resolution with regard to plant species/type information. Because the ABZ has a relatively small number of vascular plant species, DVMs with coarse vegetation resolution can often be applied across large extents due to the similarity of genera within plant functional types (PFTs) (Sulman *et al* 2021). However, while vascular plant species diversity may be low, microsite variation in soil, hydrological, thermal, and permafrost conditions in the Arctic can lead to high heterogeneity in moss, lichen, and vascular plant communities (Le Roux *et al* 2013, Mallen-Cooper *et al* 2021, Jorgenson *et al* 2022), adding challenges to parameterization and calibration. Furthermore, accumulating the data required for ecosystem inputs, and at the appropriate scale, to run a DVM is a large undertaking and makes this class of models less accessible to managers, scientists, and other practitioners, who do not have modeling experience. Even the most experienced modeler must contend with balancing the greater breadth of a global simulation from large-scale models with the detailed and more spatially variable, and more highly resolved simulation of fine scale models.

Among existing DVMs, there is a wide variety of inputs and ecosystem properties (figure 1) that are incorporated, and choosing which properties to represent is critical to model function. The built-in assumptions of each model inform the scope of its findings, but the functions and assumptions of each model are not always apparent from a review of the literature or codebase, and detailed technical model descriptions and user guides are not always available or accessible. The original intention of a model, or its foundation, frequently carries over as its strongest asset (e.g. a gap dynamics model is very good at simulating stand level tree growth and mortality; Shugart *et al* 2020). However, many models that share the same lineage have diverged since initial development to target specific processes or locations (Shugart and West 1977, Urban *et al* 1990, Yan and Shugart 2005, Shuman *et al* 2014, Brazhnik and Shugart 2016, Foster *et al* 2016). These model descendants often adjust the inputs and parameterization to their specific needs and various submodules, such that models that share origins may have divergent goals (Fisher *et al* 2018b), making ensemble model assessments more challenging. However, by bringing various model lineages to the ABZ, models must be adapted to the new system and model convergence intensifies the diversity of model and submodules being run in the region.

DVMs are powerful tools, yet challenging to implement. The goal of this paper is to demystify a collection of 18 commonly used DVMs that have been implemented across the North American boreal forest and tundra. Our specific objectives are:

- (1) To summarize and clarify ecosystem properties and processes being simulated in different DVMs for users to more easily determine which model(s) would be best suited to answer their research questions.
- (2) To review the literature to determine what types of questions have been asked using DVMs to highlight the breadth of application across the ABZ.
- (3) To survey practitioner opinion to inform future model development and application.

2. Methods

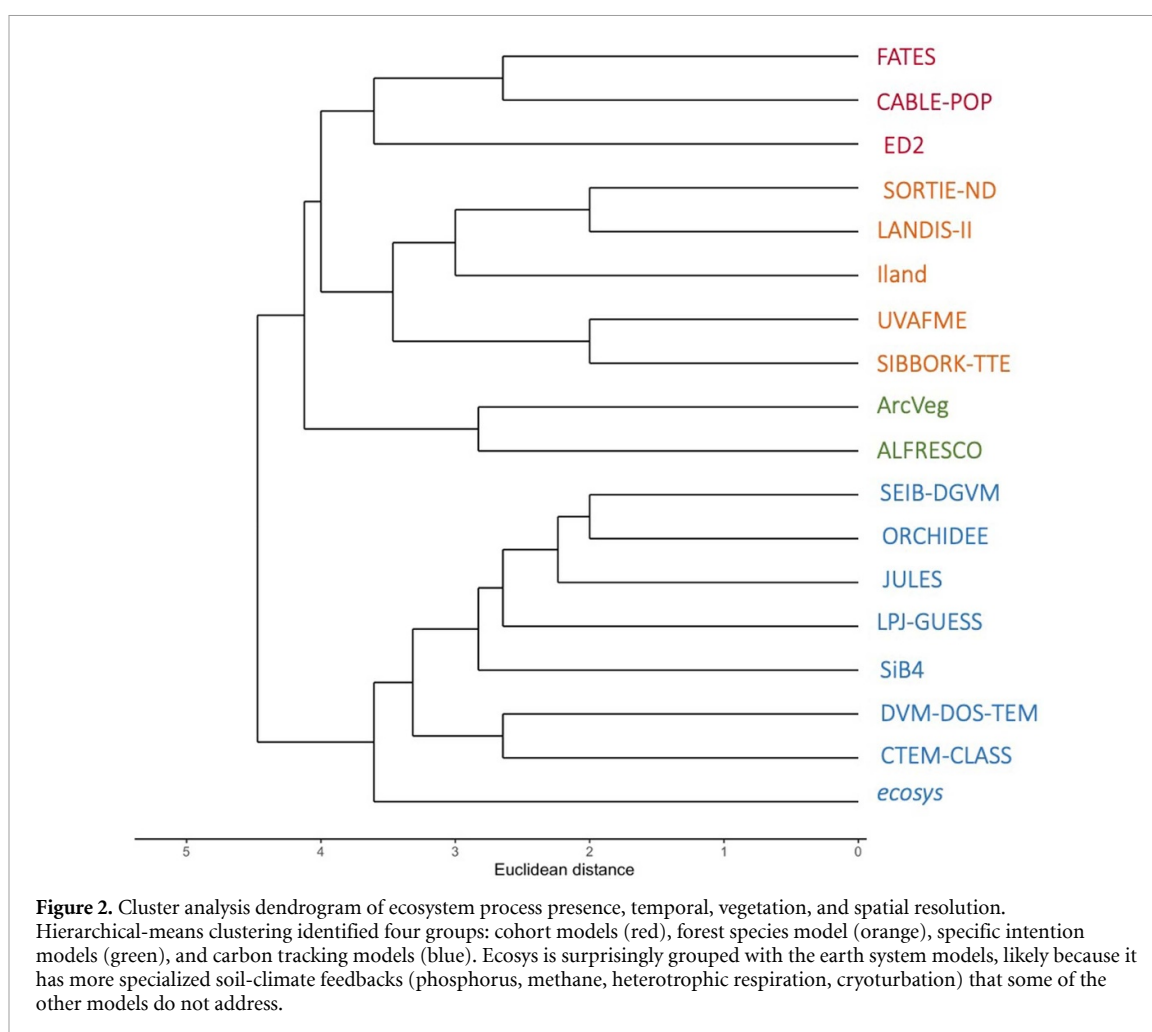
2.1. Model ecosystem properties

Model selection was based on two criteria: (1) that the model fit our definition of a DVM (i.e. has the ability for vegetation composition and distribution to change over the simulated landscape as a response to environmental forcings), and (2) that the model be applied within the North American ABZ to study vegetation dynamics or impacts thereof published over the past two decades. We found eighteen models that fit these criteria (figure 2). Models were found via literature search and review using Web of Knowledge/Web of Science, Google

Scholar, expert knowledge from the NASA Arctic-Boreal Vulnerability Experiment (ABoVE) Science Team. Once established that the model fit our criteria, information was collected through Web of Knowledge/Web of Science and Google Scholar (search terms included the model name and/or abbreviation with each of the following: Arctic, Boreal, Alaska, Canada); additionally, model websites, manuals, and technical documentation were reviewed when available. The search was finalized in June 2023. The literature search prioritized sources with model descriptions and papers showing the different applications of DVMs and their input and simulated ecosystem properties. Each DVM was reviewed and categorized based on a suite of 22 ecosystem properties (based on their documented importance from previous observational studies in determining vegetation function, composition, structure, and competition; figure 3), as well as model resolution parameters addressing spatial, temporal, and vegetation resolution. For our purposes, an ecosystem property was a state variable or process that could impact vegetation growth, reproduction, competition, or spread on the landscape; the properties were divided into categories as being a characteristic of soil (soil moisture, nitrogen, active layer depth/permafrost, heterotrophic respiration, cryoturbation, phosphorus), plant growth (succession, litterfall, light competition, seed dispersal, photosynthesis), disturbance (fire, browse herbivory, insect damage, pathogens), or land-atmosphere interactions (evapotranspiration, precipitation form, albedo, methane, CO₂ fertilization). The ecosystem properties were marked as present or absent, along with vegetation, temporal, and spatial resolution (appendix 1). The resulting matrix was analyzed using hierarchical cluster analysis to identify common traits among models using the `hclust` function (default settings, `stats` package; Bugmann and Seidl 2022) in R (4.2.1 R Core Team 2022). Using Euclidean distance, the cluster analysis measured the dissimilarity among the models in terms of each ecosystem property they represented; we used hierarchical clustering so as to not influence the number of clusters (as would be necessary for k-means clustering). Using the silhouette method, we identified 3 clusters among the dataset as maximizing the similarity of in-group models. Once the clusters were identified, we qualitatively interpreted the results to identify common traits among the groups and further split the cluster into 2 groups to highlight certain similarities of resolution and application.

2.2. Model application review

A literature review was conducted to assess how DVMs were being applied in the ABZ. For this literature review, our criteria required that the papers: (1) be published from 2017 to 2022; (2) address the North American ABZ (e.g. could be a local analysis in the North American ABZ, or could be a global study



that highlighted a finding from the North American ABZ); (3) apply at least one of the models identified by the model properties literature review. Studies were accessed through Web of Knowledge/Web of Science and Google Scholar and were surveyed from January 2023 to April 2023 using the same search parameters as the ecosystem properties search (model name + Arctic, Boreal, Alaska, Canada). We limited our search to the six-year period to focus on the most recent modeling developments; the focus on the North American ABZ allowed us to align our literature review with the scope of our expertise surveyed in the next section. Studies were separated into two categories based on whether the research question explicitly addressed vegetation dynamics (e.g. shifts in evergreen vs deciduous cover), or they indirectly included vegetation dynamics (e.g. permafrost dynamics under climate change scenarios, as mediated by vegetation; Melton *et al* 2019).

2.3. Model process survey

Importance of each of the ecosystem properties was assessed through an online Qualtrics survey. The anonymous survey was approved by the UVA IRB-SBS (Protocol #5607); and was sent to the NASA ABoVE listserv (sent to anyone associated with

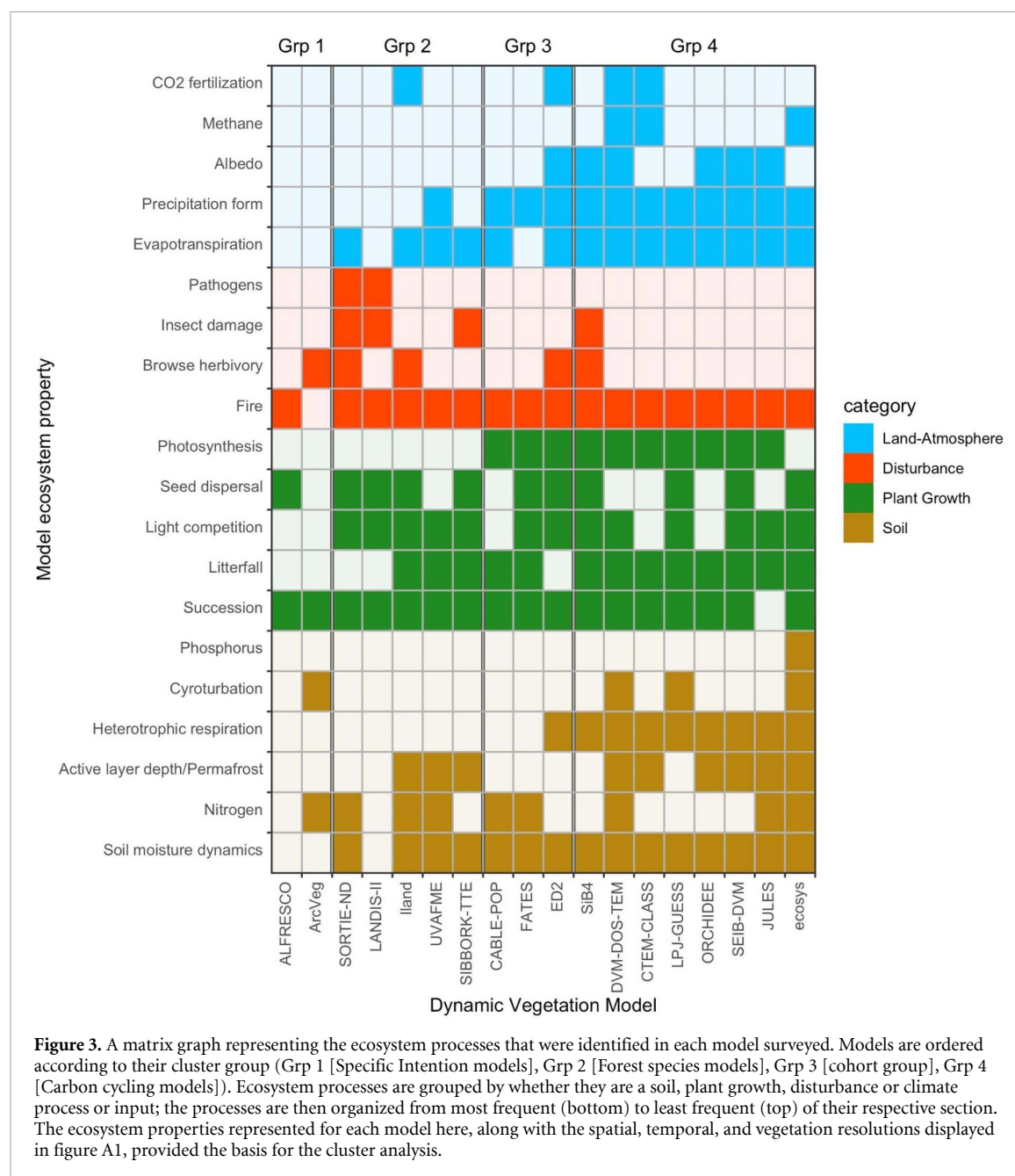
ABOVE in March 2023) to solicit practitioner opinion. The survey asked respondents to rank their most important seven properties out of the 22 ecosystem properties outlined in the *Model Ecosystem Properties* section. Air temperature was not one of the properties that could be chosen, as it was found in every model. Participants were also asked about their experience with models (e.g. collects data, creates models, reads papers, etc) and their experience level. Survey questions are available in appendix 2.

Survey results were then compared with the *Model Ecosystem Properties* review to find gaps between the processes that were deemed important by practitioners, and the processes that were being represented in the models. The survey responses were ranked and compared against the corresponding ranked order frequency of the property in the *Model Ecosystem Properties* review; when properties were tied in frequency, their rank values were averaged.

3. Results and discussion

3.1. Model ecosystem properties

The Arctic-Boreal ecosystems simulated by models are extremely complex (figure 1), and there will always be a balance between simple and complex



representations of the target ecosystem(s). Knowing which aspects of an ecosystem are included across the 18 surveyed DVMs is important to understanding the scope, challenges, and opportunities of each model.

Each model that was reviewed had a unique suite of ecosystem properties (represented in figure 1). Some models used external temperature forcing with either hourly (e.g. Chang *et al* 2020), daily (e.g. Murphy 2014) or monthly (e.g. Foster *et al* 2019) timesteps, while others used less mechanistic representations or proxies (e.g. Rupp *et al* 2000 or Epstein *et al* 2007). Some properties were more frequently represented than others in the 18 models: fire disturbance (17 models), succession (17), soil moisture dynamics (15), litterfall (13), and light competition (13). Together, these properties represent a coarse

rendering of growth, mortality, and ontogeny. Our analysis was limited to looking at the presence of ecosystem properties rather than the ways each model individually represented and ecosystem process; thus, some processes, like mortality, were assessed through proxy variables such as how the system recycles nutrients or responds to a disturbance. Phosphorus (1, *ecosys*; e.g. Chang *et al* 2020), pathogens (2; e.g. Murphy 2014, Boulanger *et al* 2018), methane (3; e.g. Arora *et al* 2018, Chang *et al* 2020, Arndt and Natali 2022) and the presence of herbivory (5; e.g. Murphy 2014, Yu *et al* 2017, Longo *et al* 2019, Haynes *et al* 2020, Hansen *et al* 2021) were the least common ecosystem properties addressed (figure 3).

The models represented in this review aggregated into four main groups from the cluster analysis (figure 2): models with a specific intention

(ALFRESCO [fire], and ArcVEG [nitrogen]); the forest-species group (SIBBORK-TTE, UVAFME, iLand, LANDIS-II, SORTIE-ND); the cohort group (ED2, CABLE-POP, FATES); and the carbon cycling group (*ecosys*, SiB4, DVM-DOS-TEM, LPJ-GUESS, ORCHIDEE, CTEM-CLASS, JULES, SEIB-DVM). These models have all been modified from their original version, frequently from different biomes to the ABZ, to generate predictions of the Arctic-Boreal ecosystems (*see next section*). The underlying mechanics of the original model family and architecture were persistent in their grouping, with some outliers addressed below (Bugmann 2001, Shugart *et al* 2018).

3.1.1. Specific intention models

The specific intention models group consisted of ArcVeg, ‘a nutrient based, plant community and ecosystem model’ (Epstein *et al* 2000) and ALFRESCO, ‘a frame-based, spatially explicit fire model’ (Rupp *et al* 2000, Hewitt *et al* 2016, Melvin *et al* 2017, www.frames.gov/catalog/7132). These models were mainly unified by their parsimony, rather than the overlapping ecosystem properties they represent. ArcVeg was initially conceived as a way to simulate the impacts of climate change and herbivory (from caribou) across the Arctic tundra with vegetation dynamics driven by the nitrogen cycle (Epstein *et al* 2000, Yu *et al* 2017). Daanen *et al* (2008) added a cryoturbation element to address the localized effects of non-sorted circles (frost boil). ALFRESCO was designed to focus on the impacts of fire disturbance and seed dispersal in Alaska (Rupp *et al* 2000). ALFRESCO utilizes an ecosystem-level vegetation resolution, but is able to cycle through the expected stages of fire-adapted vegetation succession. ArcVeg and ALFRESCO simulated the impact of increased temperatures using growth periods (see Epstein *et al* 2000) and map inputs (see Rupp *et al* 2000), respectively, to streamline the manipulation of temperature in their simulations. By employing simple and robust approaches to shifts in climate, the two models are potentially easier to apply.

3.1.2. Forest species models

The forest species model group contained SIBBORK-TTE, ‘an individual-based, spatially explicit, gap model’ (Brazhnik and Shugart 2016; <https://github.com/SIBBORK/SIBBORK>), UVAFME, ‘an individual-based gap model’ (Foster *et al* 2019, 2022, <https://uvafme.github.io/>), iLand, ‘a multiscale processed-based model’ (Seidl *et al* 2012, Hansen *et al* 2021, 2023, <https://iland-model.org/startpage>), LANDIS-II, ‘a landscape change model’ (Scheller and Domingo 2005, Boulanger *et al* 2017, 2018, Boulanger *et al* 2022, www.landis-ii.org/), and SORTIE-ND, ‘an individual-based forest simulator’ (Murphy 2014, Maleki *et al* 2019, 2021, www.sortie-nd.org/). Plant growth processes are well represented across all models, but especially within the forest species models.

This group is uniquely driven by each model having species-level vegetation resolution for trees; UVAFME and SIBBORK-TTE both have additional PFT representations within their models for non-trees (Foster *et al* 2022, 2021). The fine vegetation resolution limits the potential geographic extent of these models, and thus many represent local areas where the species distribution is generally known. Both UVAFME and SIBBORK can be run at larger scales directly or gridded mapping approaches and/or high computing power. The forest-species group also prioritized a light competition growth model over a biochemical photosynthesis (carbon accounting) process. The models bypassed the photosynthesis mechanism and calculated growth potential directly from the light input (Scheller and Domingo 2005, Seidl *et al* 2012, Murphy 2014, Brazhnik and Shugart 2015, Foster *et al* 2019). Additionally, these models are resolved at monthly (for climate inputs), or annual time-steps (for biomass outputs; Seidl *et al* 2012, Brazhnik and Shugart 2016, Boulanger *et al* 2017, Foster *et al* 2019); whereas SORTIE-ND was resolved at only the annual timestep (Maleki *et al* 2019, 2021).

The forest species models have the greatest diversity and inclusion of ecosystem disturbances (figure 3). Within the disturbance processes category, each forest model had a fire module, but LANDIS-II (Boulanger *et al* 2018) and SORTIE-ND (Murphy 2014) were the only two models to address forest pathogens. LANDIS-II, SORTIE-ND, and UVAFME are able to run simulations on insect pests, such as the spruce budworm (Maleki *et al* 2019) and spruce beetle (Steenberg *et al* 2013, Foster *et al* 2019). Browse herbivory was addressed by just two of the forest species models (Murphy 2014, Hansen *et al* 2021). The high representation of disturbance by this group was likely tied to their higher spatial and vegetation resolution, and the importance of disturbances in the boreal forests in general. A fire can be assumed to affect all the vegetation within a model pixel; however, a finer scale disturbance, such as the spruce budworm, requires differentiation in tree species and size (Werner *et al* 2006) to mimic pest preferences, but also a higher spatial resolution (hectares) to accurately represent the extent of damage. The forest species models, with their finer spatial and vegetation resolution, are thus better suited to simulating fine scale disturbances such as forest insect outbreaks and pathogens.

The models represented in the forest species group specialize in forest growth, with some adding other PFTs to better account for community composition and understory vegetation in the model adaptation to the ABZ (Foster *et al* 2019, 2021). They are well suited to the ABZ because of the focused spatial resolution, especially across the Arctic-Boreal ecotone, where there is high landscape heterogeneity and rapid shifts in vegetation cover (Holtmeier and Broll 2019). Increasing the understory representation in

the forest species models, particularly with shrub and moss PFTs, will increase their predictive power. With such improvements, these models could be utilized to predict Arctic shrubification, a well-documented result of climate warming (McManus *et al* 2012, Myers-Smith *et al* 2015, 2020, Ackerman *et al* 2018, Reid *et al* 2022). Additionally, representing a moss PFT that can influence soil insulation will increase reliability of belowground simulations (Chen *et al* 2019).

Within the forest species group, there was some geographic separation in where the models were being applied. LANDIS-II and SORTIE-ND have been primarily applied in the boreal forest of eastern Canada (Bose *et al* 2015, Boulanger *et al* 2018, 2017, Maleki *et al* 2019, 2021, Boulanger and Puigdevall 2021, Molina *et al* 2022), while UVAFME and SIBBORK-TTE have been primarily being applied in northwestern Canada and Alaska (Foster *et al* 2019, 2022). This pattern is likely an artifact of specific project focus rather than model capability.

3.1.3. Cohort models

The cohort group models were ED-2 ‘the Ecosystem Demography model’ (Longo *et al* 2019, <https://github.com/EDmodel/ED2>), FATES, ‘a cohort model of vegetation physiology, growth, and dynamics’ and companion model to CLM5.0 (Lambert *et al* 2022, <https://fates-users-guide.readthedocs.io/en/latest/index.html>), and CABLE-POP, a ‘tree demography and landscape structure model’ (Haverd *et al* 2014). The cohort group was largely unified by the utilization of PFTs further classified by growth stages (cohorts). These models have elements of both the forest species models, such as defined disturbance regimes, while also having more detailed representation of land-atmosphere interactions (figure 3). All three of the cohort models can address precipitation form (Haverd *et al* 2014, Fisher *et al* 2015, Longo *et al* 2019, Kim *et al* 2021), which is a critical and changing climate property. The interaction of snow with vegetation on the landscape and shift from snow to rain, especially in the shoulder seasons have large impacts on vegetation during the growing season (Barrere *et al* 2018, Addis and Bret-Harte 2019).

Employing a cohort tracking system to their PFTs allows vegetation ontogeny to factor into the simulations (Haverd *et al* 2014, Longo *et al* 2019, Li *et al* 2022). CABLE-POP was frequently used in model comparison studies, which made it unique in many ensemble studies as the only cohort model. By allowing PFTs to have higher resolution by attending to life-stage, models can better predict carbon storage, seed production, and growth accumulation, with tailored allometries for each life stage.

Within the cohort group, the ED-2 model has the finest spatial resolution; the model focuses on micro-environment and specifically tries to resolve the problem of high heterogeneity (Longo *et al* 2019). FATES and CABLE-POP have been implemented at

much larger spatial scales and resolutions, typically applied in global studies (table 2). The cohort group models did not have any applications for the direct assessment of vegetation dynamics (see next section), suggesting they are well suited to studying ecosystem properties tangential to vegetation dynamics, and that there is an opportunity to ask vegetation dynamics questions of these models. The cohort group would be well suited to answer questions pertaining to the interactions between climate and disturbance, and how the vegetation life stage interacts with climate, especially within the tundra-taiga ecotone where adult recruitment is critical to future predictions (Harsch *et al* 2009, Stevens-Rumann *et al* 2022).

3.1.4. Carbon tracking models

The carbon tracking group has the most diverse of model origins, including SEIB-DVM, ‘an individual-based Dynamic Global Vegetation Model’ (Sato *et al* 2007, <http://seib-dgvm.com/>), and SiB4, also ‘a mechanistic, prognostic land surface model’ (Haynes *et al* 2019, 2020), LPJ-GUESS, ‘a process-based global dynamic vegetation model’ (Smith *et al* 2014, <https://web.nateko.lu.se/lpj-guess/faq.html>), DVM-DOS-TEM, ‘a process based bio-geo-chemical ecosystem model’ (Euskirchen *et al* 2022, <https://github.com/uaf-arctic-eco-modeling/dvm-dos-tem>), CLASS-CTEM, ‘an earth system model with a terrestrial ecosystem model’ (Melton and Arora 2016, https://cccma.gitlab.io/classic_pages/info/ctem/), ORCHIDEE, ‘a land surface model’ (Druel *et al* 2017, Bowring *et al* 2019, <https://orchidee.ipsl.fr/>), JULES, ‘a community land surface model’ (Best *et al* 2009, 2011, Clark *et al* 2011, <https://jules.jchmr.org/>), and *ecosys*, ‘a terrestrial ecosystem biochemistry model’ (Chang *et al* 2020, <https://ecosys.ualberta.ca/>). Among the carbon tracking models, SiB4 was unique in representing browse herbivory and insect damage but does so at a coarse resolution; the rest of the group simulated fire but not browse herbivory or insects (figure 3). However, the carbon tracking models all represented photosynthesis, heterotrophic respiration, and evapotranspiration.

The carbon tracking models also each included different precipitation forms, and frequently included snowpack dynamics (Burke *et al* 2017, Krause *et al* 2019, Gädeke *et al* 2020, Chadburn *et al* 2022, Shirley *et al* 2022a). The ability to track liquid vs. solid precipitation is critical for modeling in the ABZ, as the recent shift in precipitation from snow to rain has cascading effects on vegetation response (Callaghan *et al* 2011, Addis and Bret-Harte 2019, Rees *et al* 2020).

The majority of the carbon tracking models included in this study have fine temporal resolutions, either daily (or finer) or monthly; however, there is a tradeoff for many in spatial scale. These models, with the exception of *ecosys* and SEIB-DVM, have largely been applied at $0.25^\circ \times 0.25^\circ$ or coarser resolution

(Slevin *et al* 2017, Gädeke *et al* 2020, Zhang *et al* 2014, Euskirchen *et al* 2022, Shirley *et al* 2022a, Yu *et al* 2022); DVM-DOS-TEM represents a middle spatial resolution, typically running at 1–4 km² (Euskirchen *et al* 2016). This tradeoff is typical of many land-atmosphere submodules, and enables a larger extent of application; however, it may be at the expense of spatial resolution. A coarse spatial resolution risks homogenizing the highly heterogeneous landscape of the ABZ and ecotone especially (Holtmeier and Broll 2019). All of these models maintained PFT-level vegetation resolution, but the number of PFTs defined by each model included in this study varies from 5 to 15 (Clark *et al* 2011, Haynes *et al* 2020).

Ecosys and SEIB-DVM were surprising inclusions in the carbon tracking group, which mostly highlights land-atmosphere interactions (figure 3). Potential, their inclusion of heterotrophic respiration aligned these two models with the carbon tracking models (Shirley *et al* 2022b, Yu *et al* 2022); both models simulate active layer depth (Mekonnen *et al* 2018a, Sato *et al* 2020), and *ecosys* can also track methane fluxes, along with CLASS-CTEM and DVM-DOS-TEM (Grant *et al* 2017, Arora *et al* 2018, Briones *et al* 2022). These properties, along with snowpack, are critical to simulating carbon emissions and resolving the status of below-ground hydrology, temperature, nutrient cycling and subsequent vegetation type and success. The belowground processes that the carbon tracking models simulate are critical to accurately predicting how the ABZ will respond aboveground.

3.1.5. Evaluation of model properties

The 18 models surveyed were grouped largely by their vegetation resolution (forest species vs cohort groups vs general PFTs in the carbon tracking groups). This breakdown among the forest species, cohort, and carbon tracking groups highlights the importance of vegetation representation in the models.

As the Arctic is a dynamic system in the process of adapting to a new climate, complex models are needed to evaluate and accurately project change. With each model representing a unique suite of ecosystem properties, the importance of each property in their respective models weighs differently on the model processes and outputs. For example, while the models (almost) all include temperature or fire, these properties are weighted differently in each model depending on internal structure. Thus, it is important for future studies to test an ensemble of models to understand the breadth of possibilities for the future ABZ.

In the Arctic, vegetation growth is especially limited by hydrological processes that are highly variable, difficult to model, and even more difficult to ground truth or remotely sense (Campbell *et al* 2021, Miner *et al* 2022). Permafrost and active layer depth (Miner *et al* 2022), snow depth (Barrere *et al* 2018), and water logging (Simard *et al* 2007) govern plant distribution

and growth rates, but are not universally represented in models. When these properties are included, they are usually resolved at spatial scales too coarse to adequately capture realistic heterogeneity (figure 3; Siewart *et al* 2021). Thus, a model that does not factor in the shifts in dynamic belowground hydrology might have a skewed representation of vegetation growth as compared to one that does. Presently, models that addressed belowground processes in the Arctic can simulate permafrost dynamics (Clark *et al* 2011, Druel *et al* 2017, Arora *et al* 2018, Foster *et al* 2019, Sato *et al* 2020, Euskirchen *et al* 2022, Hansen *et al* 2023, 2021); however, some of the models with permafrost submodules operate at scales too great for permafrost variability (Krogh and Pomeroy 2021, Siewart *et al* 2021).

One limitation of many models is that the ecosystem processes they attempt to simulate occur at finer spatial scales than the inputs that are available (e.g. running a model on a m² resolution, but the input is 250 m²; (Fritsch *et al* 2020)). This pseudo-high resolution may be appropriate for some ecosystem processes, if the appropriate stochasticity is simulated. For example, SoilGrids data are resolved at 250 m² (Poggio *et al* 2021), but the soil carbon variation across that area would be misrepresented by a single value. While all the model scales could benefit from increasing resolution, the nuances of noise would be more pressing for the high spatial resolution models in the forest species group. Sub-meter belowground properties, such as active layer depth, could be highly variable within a site and would dictate which species could exist in different areas (Duchesne *et al* 2018, Heijmans *et al* 2022, Foster *et al* 2022, Shirley *et al* 2022b).

3.2. Model application review

Our literature review yielded 48 studies that applied DVMs within the North American ABZ since 2017. Twenty-two studies focused on shifts in vegetation (table 1); they range in location, scale, and model manipulation (e.g. climate change, harvesting), as well as single model vs. ensemble model approaches. Only two studies addressed direct management questions about harvesting (Maleki *et al* 2021) and spruce budworm outbreak (Maleki *et al* 2019). Many of the studies were focused on the future species composition. Studies that investigated climate change scenarios found that evergreen trees/PFTs are likely to do poorly in warming climates, and broadleaf trees/PFTs are likely to do well (Boulanger *et al* 2017, 2018, Chaste *et al* 2019, Foster *et al* 2019, Mekonnen *et al* 2019, Cadieux *et al* 2020, Boulanger and Puigdevall 2021, Foster *et al* 2022). Twenty-six studies addressed other research questions, leveraging the abilities of models that simulate dynamic vegetation to parse interactions among ecosystem processes that are indirectly related to vegetation growth (e.g.

Table 1. Studies that used models to investigate shifts in vegetation. Studies are briefly summarized by their manipulation and location and overall result.

Model	Location(s)	Vegetation resolution	Model manipulation	Vegetation result	Citation
ALFRESCO	Alaska and NW Canada: Western Alaska	Ecosystem	Climate change: A1B	Decrease in late successional forest types and increase in early successional deciduous forests	Euskirchen <i>et al</i> (2016)
ArcVeg	Circumpolar tundra	PFT	Climate change: RCP 8.5	Southern subzones increased in biomass; combined net effect of herbivory and climate change is still net increase in biomass	Yu <i>et al</i> (2017)
CLASS-CTEM	Circumpolar	PFT	Model comparison	Increase in plant area index across most of Arctic. Larger increase when using CTEM	Teufel <i>et al</i> (2019)
CLASS-CTEM	North America	PFT	Model comparison	CTEM-CLASS overestimated vegetation; After 1960s, CO ₂ fertilization and climate warming increased fraction of tree PFTs	Shrestha <i>et al</i> (2017)
<i>ecosys</i>	Alaska boreal forest	PFT	Climate change: RCP 8.5 Fire module	Evergreen PFTs decreased in climate change + fire scenario; Evergreen PFT and deciduous able to keep pace in fire no climate change scenario	Mekonnen <i>et al</i> 2019
iLand	Alaska	Species	Climate change: RCP 8.5; Also tested seed dispersal, fire regimes, browse pressure	Mixed forest and black spruce forests were maintained when fire return intervals were long, deciduous browse pressure was high and seed source was distant	Hansen <i>et al</i> 2021
JULES, LPJ-LM, LPJGuess, SEIB DGVM, CABLE-POP	Global	PFT	Model comparison Climate Change: RCP 8.5	Tree mortality should decrease in boreal, but models had the least agreement in boreal forest	Yu <i>et al</i> 2022
LANDIS-II	Boreal plains of NE Alberta Canada	Ecosystem	Climate change: RCP 2.6, 4.5 & 8.5 Harvesting pressure	Under RCP 4.5 & 8.5: Increase in treeless area, decrease in conifer forest. Slight increase in deciduous forest; climate change had greater effect than harvesting	Cadieux <i>et al</i> 2020
LANDIS-II	Southern Canada boreal transition zone	Ecosystem	Climate change: RCP 2.6, 4.5 & 8.5	Shift towards younger forests dominated by a few species, especially early to mid successional species; decrease in coniferous species.	Boulanger <i>et al</i> (2018)
LANDIS-II	Southern Canada boreal transition zone	Ecosystem	Climate change: RCP 2.6, 4.5 & 8.5	Decrease in boreal species, increase in temperate species, especially under RCP 8.5	Boulanger <i>et al</i> (2017)
LANDIS-II	Boreal forest in Quebec, CAN	Species	Climate change: RCP 8.5 Disturbance type	Increase in non-fire adapted species in RCP8.5 scenarioHardwoods and mixed forests were favored after forest management disturbance while conifers were favored after fire disturbance.	Molina <i>et al</i> (2022)
LANDIS-II	Quebec, CAN	Ecosystem	Climate change: RCP 2.6, 4.5 & 8.5	Decrease in boreal conifers. Hardwoods would increase but not enough to completely offset the loss of biomass. Black spruce would disappear in west boreal by 2150 under RCP 8.5	Boulanger and Puigdevall (2021)

(Continued.)

Table 1. (Continued.)

Model	Location(s)	Vegetation resolution	Model manipulation	Vegetation result	Citation
LPJ-LMFire (LPJ-GUESS + SPITFIRE)	Eastern Canadian Boreal Forest	PFT	Climate Change: RCP 4.5 and 8.5	Increase in <i>Populus</i> in southern ecozones and co-dominance with <i>Picea</i> in northern	Chaste <i>et al</i> (2019)
LPJ-LMFire (LPJ-GUESS + SPITFIRE)	Eastern Canadian Boreal Forest	PFT	Calibrating model	Overestimated <i>Picea</i> and <i>Populus</i> biomass across region; underestimated <i>Pinus</i> and <i>Abies</i> in the north but underestimated in the south	Chaste <i>et al</i> (2018)
ORCHIDEE	Circumpolar (CAVM)	PFT	Climate Change: RCP 4.5 and 8.5	Boreal band, trees coverage increases (42% and 68%) at the expense of shrub cover; in Arctic band; trees increase 120% and 250% in the two scenarios; at the expense of shrubs and grasses.	Druel <i>et al</i> (2019)
SEIB DGVM	Global	PFT	Light vs Water gathering biomass	Total vegetation increased 119 Pg (1901–2015), 97% due to light gathering biomass; water gathering biomass increases most in boreal zones	Tong <i>et al</i> (2022)
SEIB DGVM	Circumpolar	PFT	Model Comparison	Model predicted increase in growth while RWI based model	Tei <i>et al</i> (2017)
SEIB DGVM + ensemble	North America	PFT	Climate Change: RCP 8.5 Model Comparison Climate Change: RCP 8.5 vs Last Glacial Maximum and modern historic	predicted spatial variability in tree growth trends Increase in <i>C₄</i> species but models disagree where	Still <i>et al</i> (2019)
SORTIE-ND	Lake Duparquet Research and Teaching Forest, Quebec, CA.	Species	Spruce budworm outbreak	Cedar infills into old stands; spruce budworm significantly affected balsam fir	Maleki <i>et al</i> (2019)
SORTIE-ND	Lake Duparquet Research and Teaching Forest, Quebec, CA.	Species	Clear cutting	Clear cut: reset of succession and aspen dominance—Partial harvest: maintain general composition of original stands	Maleki <i>et al</i> (2021)
TEM	Boreal Alaska and Canada	PFT	Historical carbon balance	After 25 years following fires, difference in vegetation carbon decreased to 773.0–1242.2 g C m ⁻² from the initially removed carbon 1512 g C m ⁻²	Zhao <i>et al</i> (2021)
UVAFME	Tanana River Basin, AK, USA	Species	Climate change; RCP 4.5 & 8.5	Overall decrease in spruce forest and increase in deciduous forest. Greater increase in biomass under RCP 4.5 than under RCP 8.5	Foster <i>et al</i> (2019)
UVAFME	AK and Western Canada	Species	Climate change; RCP 4.5 & 8.5	RCP 4.5 Total biomass will slightly increase and the fraction of deciduous areas will slightly increase. RCP 8.5: total biomass will decrease and fraction of deciduous areas will increase greatly	Foster <i>et al</i> (2022)

methane sinks, influence of microtopography, phenology of carbon source/sink, peatland source/sink, carbonyl sulfide, snow phenology, etc; table 2). With increasing model capabilities, the studies that implicitly assessed vegetation dynamics (table 2) demonstrate the versatility of a DVM to increase our understanding of different responses and interactions of ecosystem properties with changing vegetation.

While difficult to simulate at larger scales, the models were frequently used to study belowground properties, such as permafrost (Burke *et al* 2017, Melton *et al* 2019, Shirley *et al* 2022a), and soil carbon (Larson *et al* 2022), methane cycling (Grant *et al* 2017), and peat accumulation (Chaudhary *et al* 2017, 2020, Chadburn *et al* 2022, Chaudhary *et al* 2022, Mekonnen *et al* 2022, Shirley *et al* 2022a). Model comparisons (both model sensitivity and ensemble model comparisons) were a frequent research goal, but were limited to large-scale models, almost all of which were in the carbon tracking group (CABLE-POP, CLASS-CTEM, ED2, JULES, LPJ-GUESS, ORCHIDEE etc; Burke *et al* 2017, Krause *et al* 2019, Rogers *et al* 2019, Gädeke *et al* 2020, Yang *et al* 2020). The *ecosys* model stood out particularly as a model that was able to address many different types of questions about Arctic-Boreal ecosystems, such as how climate change and fire will influence vegetation (Mekonnen *et al* 2019), how CO₂ and CH₄ are affected by tundra polygons (Grant *et al* 2017), and the effects of microtopography and soil heterogeneity on vegetation (Mekonnen *et al* 2018b, 2021, Shirley *et al* 2022b). The suite of *ecosys* papers demonstrates how creative questions can be asked of models to focus on different ecosystem properties and the subsequent effects on vegetation, highlighting the dynamism of Arctic vegetation in a changing climate. It is important for models to predict what the ABZ future vegetation will look like, but knowing how ecosystem property interactions are likely to shift under stress is equally important.

One limitation that the model application review highlighted is how individual models tend to be primarily used by single research groups. A research group can produce many studies using one model, but the models might not be readily transferred, or even transferable, making versatility a challenge. Model transference can be limited by code availability, code complexity and language (i.e. how steep is the learning curve), and input data requirements. The ensemble model comparison approach would increase reproducibility and connection among research teams; however, it can be limited by the internal structure of each model and whether the required inputs are available, especially for the individual-based gap model structures. An ensemble of models can yield many different outcomes and enable a more reliable, averaged outcome with uncertainties. However, while both managers and modelers would benefit from a suite of models to predict future

scenarios, parameterizing models is both time and computationally intensive.

3.3. Model process survey

The survey asked respondents to select their top seven out of 22 ecosystem properties (same properties listed in figure 3; questions in appendix 2). One hundred fifty-five respondents from the NASA ABoVE listserv completed the survey over a two-week period (13–27 March 2023). The respondent demographic included a mix of advanced (20%, 31 respondents), intermediate (41%, 65 respondents), and novice (34%, 54 respondents) practitioners. Of the respondents, 51% (79 respondents) collected data that could be used in models, 24% (37 respondents) worked to develop models, 31% (48 respondents) ran models, and 63% (98 respondents) read papers about models (multiple responses were accepted for this question). We found no trends between respondent experience and/or application and the ecosystem properties they selected.

The top three ecosystem processes selected as important to DVMs were soil moisture dynamics, fire, and active layer depth/permafrost (table 3). Soil moisture properties, and active layer depth, create a highly heterogeneous belowground matrix which influences vegetative community and individual success (Limpens *et al* 2021, Kemppinen *et al* 2021, Heijmans *et al* 2022); however, soil moisture is already well represented, simulated in 15 of the models. These factors (i.e. soil moisture and active layer depth), while important for larger-scale models, are critical for the finer-scale, local models. Fire, nearly universally represented in the models (17), represents a much larger scale disturbance that influences landscape structural heterogeneity, especially in the boreal forest (Mack *et al* 2011, 2021, Reid *et al* 2022). Of these three most ‘in demand’ modeled ecosystem properties as ranked by respondents, active layer depth/permafrost had the largest discrepancy between its practitioner demand and the number of models in which it was incorporated (table 3). This demand suggests that there is an important modeling gap to be filled, which should increase the confidence of model predictions. Including active layer depth and permafrost in more models would be a positive step to more accurately capture ABZ vegetation dynamics; however, these data are spatially and temporally limited and challenging to accurately model.

The survey identified five ecosystem processes that were in high practitioner demand relative to the number of models that had the process incorporated (i.e. supply). Active layer depth/permafrost and thermokarst had the highest difference between practitioner demand and model supply (3 vs. 12 rank, and 13 vs. 22, table 3). The other processes that are in practitioner demand (insect outbreaks, nitrogen cycling, and herbivory) had lower disparities between demand and supply (differences in rank of 6.5–3.5). Many of

Table 2. Model studies that focused on other topics in the North-American ABZ but utilized the dynamic vegetation capabilities of each model.

Model	Location	Vegetation Resolution	Paper focus	Citation
ALFRESCO	Alaska boreal forest	Ecosystem	Wildfire	Melvin <i>et al</i> (2017)
CABLE-POP,	Global	PFT	Model comparison	Yang <i>et al</i> (2020)
CLASS-CTEM, JULES,				
LPJ-GUESS,				
ORCHIDEE,				
ORCHIDEE-MICT, etc.				
CABLE-POP,	Global	PFT	Model comparison; carbon flux	Krause <i>et al</i> (2019)
LPJ-GUESS, LPJ				
CLASS-CTEM	Circumpolar	PFT	Permafrost	Melton <i>et al</i> (2019)
ecosys	Alaska	PFT	Soil organic carbon and wildfire	Mekonnen <i>et al</i> (2022)
ecosys	Barrow Experimental Observatory, AK, USA	Tundra polygon type	CO ₂ and CH ₄	Grant <i>et al</i> (2017)
ecosys	North American Arctic	PFT	Microtopography	Mekonnen <i>et al</i> (2018a)
ecosys	Kougarok Hillslope, AK	PFT	Microtopography	Mekonnen <i>et al</i> (2021)
ecosys	Alaska	PFT	Phenological source/sink	Shirley <i>et al</i> (2022a)
ecosys	Seward Peninsula, AK	PFT	Soil and permafrost heterogeneity	Shirley <i>et al</i> (2022a)
ecosys	Alaska	PFT	Machine learning comparison	Shirley <i>et al</i> (2023)
ED2	Imnavait Creek watershed, Alaska	PFT	Soil carbon	Larson <i>et al</i> (2022)
ED2	Alaska	PFT	Snow phenology	Kim <i>et al</i> (2021)
ED2, JULES, ensemble	Barrow Environmental Observatory (BEO), AK	PFT	Photosynthesis	Rogers <i>et al</i> (2019)
JULES	Global	PFT	GPP comparison	Slevin <i>et al</i> (2017)
JULES	Circumpolar	PFT	Peatlands	Chadburn <i>et al</i> (2022)
JULES, ORCHIDEE, LPJ	6 largest Arctic watersheds	PFT	Hydrology—river discharge	Gädeke <i>et al</i> (2020)
LPJ-GUESS	Circumpolar	PFT	Peatlands	Chaudhary <i>et al</i> (2020)
LPJ-GUESS	Circumpolar	PFT	Peatlands	Chaudhary <i>et al</i> (2022)
LPJ-GUESS	Mer Bleue, Ottawa, CAN	PFT	Peatlands	Chaudhary <i>et al</i> (2017)
LPJ-GUESS	Circumpolar	PFT	Sea ice ~ vegetation feedback	Zhang <i>et al</i> (2014)
ORCHIDEE and JULES	Circumpolar	PFT	Climate permafrost feedback	Burke <i>et al</i> (2017)
SEIB DGVM	Canada, Austria, Switzerland, Panama	PFT	Nonstructural carbon	Ninomiya <i>et al</i> (2023)
SiB4	Circumpolar	PFT	Carbonyl sulfide	Vesala <i>et al</i> (2022)
SiB4	Global	PFT	Carbonyl sulfide	Kooijmans <i>et al</i> (2021)
TEM	Alaska	PFT	Model sensitivity	Euskirchen <i>et al</i> (2022)

the ecosystem processes were in lower demand than model supply, suggesting that the models are mostly satisfying practitioner use and application for these properties.

Thermokarst is an important element of landscape change and indicates a sudden structural failure of the permafrost due to thaw (Miner *et al* 2022). While the demand for thermokarst in DVMs was not large, the lack of representation in the

models of thermokarst presents an opportunity for development. Vegetation can both insulate permafrost (Turetsky *et al* 2012, Domine *et al* 2022), and exacerbate loss (Kropp *et al* 2021), making DVMs a good model type to simulate thermokarst processes. Because large thermokarst events can expose carbon and shift the source/sink status of a site (Pegoraro *et al* 2021), the inclusion of this landscape change is important to consider. Active layer cryoturbation

Table 3. Survey responses highlighting the ecosystem properties that practitioners think are most important to arctic vegetation dynamics. The difference column is the demand column (survey respondent rank) minus the supply (model rank). The ecosystem properties are ordered by the highest difference to highlight the ecosystem model properties that are most mismatched between demand and supply. Half ranks are the result of tied rank orders being averaged.

Ecosystem model property	Survey rank	Model rank	Difference
Active layer depth	3	12	−9
Thermokarst	13	22	−9
Insect outbreak	10	16.5	−6.5
Nitrogen cycling	6	10.5	−4.5
Herbivory (browse)	11.5	15	−3.5
Precipitation and form (snow vs rain)	4	7	−3
Soil moisture dynamics	1	3	−2
Photosynthesis	7	9	−2
Phosphorus cycling	19	21	−2
CO ₂ fertilization	15.5	16.5	−1
Methane emissions	18.5	18.5	0
Fire	2	1.5	0.5
Albedo	14	13.5	0.5
Seed dispersal	9	8	1
Pathogens	21.5	20	1.5
Variable growth mechanisms	16.5	13.5	3
Cyroturbation	21.5	18.5	3
Succession	5	1.5	3.5
Evapotranspiration	8	4	4
Light competition	11.5	5.5	6
Heterotrophic respiration	17.5	10.5	7
Litterfall	20	5.5	14.5

was similarly absent from most models; however, the demand was lower, showing a practitioner preference for the larger landscape process than the smaller freeze-thaw soil cycles.

There are some ecosystem properties that are represented to a greater extent than demanded, having a greater than 6 rank order discrepancy (light competition, heterotrophic respiration, and litterfall). Light competition and litterfall are important processes to vegetation growth and thus would be expected to be commonly found in DVMs. However, we expect this result is also from a bias in question design. The IRB-SBS Study Information Sheet stated that ‘the purpose of the study is to highlight the gap between what ecosystem processes are being simulated in vegetation models and what processes are considered important to growth but have not been accounted for in vegetation modeling’. This statement could have biased respondents to select ecosystem processes that are less common in models, particularly as we have many respondents with high familiarity with model design and application. Additionally, the question was framed to ask respondents to select ecosystem properties that were important to vegetation dynamics, which may have biased the answer away from carbon tracking answers. Another cause for the over-representation of some of these processes could be an artifact from models that were designed

for lower latitudes, or global applications, where certain properties might be more fundamentally important to understanding those ecosystems. However, we do not think that these biases in question design reduce the significance of the above outcomes and what ecosystem properties were desired to improve DVMs in the ABZ.

4. Conclusion

The ABZ is a highly dynamic and heterogeneous region, and DVMs are an important tool for predicting its future. The suite of models outlined in this paper cover a breadth of ecosystem properties and temporal, spatial, and vegetation resolutions depending on the scope of the model. We offer a summary of these models to document the present state and applications of DVMs in the North American ABZ, and to serve as a future reference point in model development. The applications of these models highlight the versatility of the DVMs to simulate and understand ecosystem properties that can be difficult to otherwise approach at large scales. With computing power being alleviated as a primary limitation, DVMs are more limited by the diversity of questions and tests being asked of them and the ecosystem properties they represent. Our survey suggests that modeling permafrost-vegetation dynamics is the

next frontier in advancement and demand; developing this ecosystem property will greatly reduce uncertainties in predictions of ABZ vegetation composition and structure.

Acknowledgments

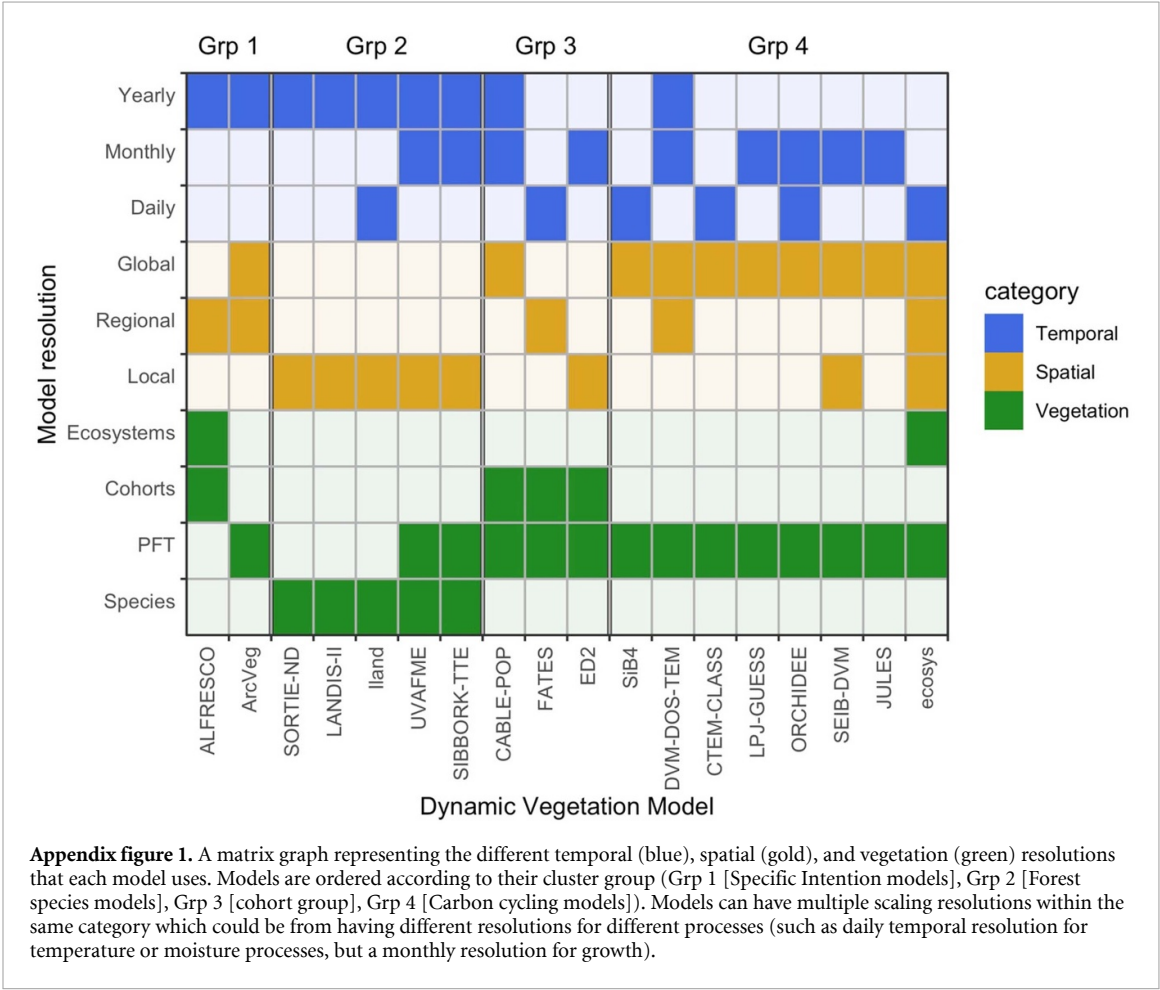
We would like to thank Shelby Lawton for allowing us to use her artwork (shelbyartworks.com, slawton623@gmail.com). We also thank all our survey participants for sharing their expert opinions. We received funding support from NASA

ABOVE (80NSSC19M0112, 80NSSC22K1247 and 80NSSC19M0111), the Gordon and Betty Moore foundation (Grant Nos. 8414) and the Audacious project (Permafrost Pathways).

Ethical statement

This human study was approved by Institutional Review Board for the Social and Behavioral Sciences (Protocol Number: 5607). All adult participants provided written informed consent to participate in this study.

Appendix 1



Appendix 2

Survey questions

1. Please select the 7 most important processes for models to explicitly represent that drive vegetation dynamics in the ABZ.

Note—temperature was not included because it is represented in all the models surveyed.

- Evapotranspiration
- CO₂ fertilization
- Litterfall
- Soil moisture dynamics
- Nitrogen cycling
- Active layer depth/Permafrost
- Pathogens
- Insect outbreak
- Methane emissions
- Seed dispersal
- Variable growth mechanisms (e.g. single stem, multi-stem, growth form)
- Heterotrophic respiration
- Precipitation and form (snow vs rain)
- Herbivory (browse)
- Photosynthesis
- Phosphorus cycling

Cyroturbation
Albedo
Light competition
Thermokarst Fire
Succession
Other

2. What is your level of engagement/comfort level with models?

Novice
Intermediate
Advanced

3. How do you primarily interact with DVMs? (Choose all that apply)

Collect data for input
Develop model (i.e. write model code)
Run model and use output
Reads model papers and applies output to other research ideas
Other.

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