

1 **Improving the representation of high-latitude vegetation**
2 **distribution in Dynamic Global Vegetation Models**
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16 **Keywords:** Area frame survey, Community Land Model, CLM4.5BGCDV, Distribution model, Earth System
17 Model, Plant functional types, Remote sensing, Vegetation types,
18

19 **Abstract.** Vegetation is an important component in global ecosystems, affecting the physical, hydrological and
20 biogeochemical properties of the land surface. Accordingly, the way vegetation is parameterised strongly
21 influences predictions of future climate by Earth system models. To capture future spatial and temporal changes
22 in vegetation cover and its feedbacks to the climate system, dynamic global vegetation models (DGVM) are
23 included as important components of land surface models. Variation in the predicted vegetation cover from
24 DGVMs therefore has large impacts on modelled radiative and non-radiative properties, especially over high-
25 latitude regions. DGVMs are mostly evaluated by remotely sensed products, less often by other vegetation
26 products or by in-situ field observations. In this study, we evaluate the performance of three methods for spatial
27 representation of present-day vegetation cover with respect to prediction of plant functional type (PFT) profiles –
28 one based upon distribution models (DM), one that uses a remote sensing (RS) dataset and a DGVM
29 (CLM4.5BGCDV). While DGVMs predicts PFT profiles based on physiological and ecological processes, DM
30 relies on statistical correlations between a set of predictors and the modelled target, and the RS dataset is based on
31 classification of spectral reflectance patterns of satellite images. PFT profiles obtained from an independently
32 collected field-based vegetation dataset from Norway were used for the evaluation. We found that RS-based PFT
33 profiles matched the reference dataset best, closely followed by DM, whereas predictions from DGVM often
34 deviated strongly from the reference. DGVM predictions overestimated the area covered by boreal needleleaf
35 evergreen trees and bare ground at the expense of boreal broadleaf deciduous trees and shrubs. Based on
36 environmental predictors identified by DM as important, three new environmental variables (e.g. minimum
37 temperature in May, snow water equivalent in October and precipitation seasonality) were selected as the threshold
38 for the establishment of these high-latitude PFTs. We performed a series of sensitivity experiments to investigate
39 if these thresholds improve the performance of the DGVM. Based on our results, we suggest implementation of
40 one of these novel PFT-specific thresholds (i.e., precipitation seasonality) in the DGVM. The results highlight the
41 potential of using PFT-specific thresholds obtained by DM in development of DGVMs in broader regions. Also,
42 we emphasize the potential of establishing DM as a reliable method for providing PFT distributions for evaluation
43 of DGVMs alongside RS.

44 **1 Introduction**

45 Vegetation plays an important role in the climate system, as changes in the vegetation cover alter the
46 biogeophysical and biogeochemical properties of the land surface (Davin and de Noblet-Ducoudré, 2010;
47 Duveiller et al., 2018). Therefore accurate descriptions of the vegetation distribution hold a key role in Earth
48 system models (ESM) (Bonan, 2016; Poulter et al., 2015). Historical and present vegetation distributions can be
49 prescribed in ESMs by means of datasets prepared from observations (Lawrence and Chase, 2007; Li et al., 2018;
50 Lawrence et al., 2011). However, in order to predict the future temporal and spatial changes in natural vegetation
51 cover and subsequently the processes, dynamics and feedbacks to the climate system, dynamic global vegetation
52 models (DGVMs) are needed.

53 DGVMs have been implemented as components of ESMs (Bonan et al., 2003) to represent long-term vegetation
54 changes by a set of parameterizations describing general physiological principles, including ecological
55 disturbances, successions (Seo and Kim, 2019) and species interactions (Scheiter et al., 2013). DGVMs represent
56 the heterogeneity of land surface processes and interactions with other components of the Earth system by
57 characterising land areas by their composition of type units defined by plant functional types (PFTs) (Bonan et al.,
58 2003; Oleson et al., 2013). PFTs are groupings of plant species with similar eco-physiological properties – which
59 express differences in growth form (woody vs herbaceous), leaf longevity (deciduous vs evergreen) and
60 photosynthetic pathway (C3 and C4) (Wullschleger et al., 2014). Even though DGVMs are being constantly
61 developed and improved to incorporate more complex plant processes (Fisher et al., 2010), and more PFTs
62 (Chadburn et al., 2015; Porada et al., 2016; Druel et al., 2017), there are still fundamental challenges for DGVMs
63 to correctly simulate the extents of PFTs that characterise boreal and Arctic ecoregions (Gotangco Castillo et al.,
64 2012). For instance, the thematic resolution (i.e. the number of classes or PFTs in a model) of high-latitude PFTs
65 is still limited (Wullschleger et al., 2014), important interactions between vegetation and fire at high latitudes are
66 still missing (Seo and Kim, 2019) which in turn has implications on forest carbon storage in high latitudes still
67 being underestimated by most DGVMs (Song et al., 2013). The large uncertainties in simulating high-latitude PFT
68 distributions may also lead to discrepancies between modelled and observed energy fluxes and hydrology (Hartley
69 et al., 2017), carbon cycles (Sitch et al., 2008) or surface albedo (Shi et al., 2018). Accordingly, systematic
70 evaluation of PFT distributions modelled by DGVMs is required to improve the DGVMs and, subsequently, to
71 reduce uncertainties in estimates of climate sensitivity and in predictions by ESMs.

72 Remote sensing (RS) is often used for evaluation, benchmarking and improvement of parameters of DGVMs (Zhu
73 et al., 2018). RS products are commonly used to describe vegetation cover using vegetation classes derived from
74 multispectral images based on vegetation indices, such as the normalized difference vegetation index (NDVI) (Xie
75 et al., 2008; Franklin and Wulder, 2002). For evaluation, RS products are translated into distributions of the PFT
76 classes used in the DGVMs (Lawrence and Chase, 2007; Poulter et al., 2011). However, inconsistencies between
77 various available RS-based land cover or vegetation products (Majasalmi et al., 2018) as well as mismatch between
78 the spatial resolution in RS observations and the spatial heterogeneity of vegetation patches (Myers-Smith et al.,
79 2011; Lantz et al., 2010) have been reported. The fact that benchmarking DGVMs only to these RS-based products
80 may lead to different conclusions in ESMs (Poulter et al., 2015), motivates for exploring other vegetation products
81 as a supplement to RS.

82 Among the less explored methods to generate wall-to-wall vegetation cover predictions is distribution modelling.
83 Distribution models (DMs) are most often used to predict the distribution of a target, by establishment of statistical

84 relationship between the target (response) and the environment (predictors) (e.g. Halvorsen, 2012). The most
85 common use of DM in ecology is for prediction of species distributions (Henderson et al., 2014), but DM methods
86 have proved valuable also for prediction of targets at higher levels of bio-, geo- or eco-diversity (i.e. vegetation
87 types and land-cover types) (Ullerud et al., 2016; Horvath et al., 2019; Simensen et al., 2020). DM methods are
88 inherently static, in contrast to the dynamic DGVMs (Snell et al., 2014). Nevertheless, they may be a useful
89 corrective to DGVMs by providing insights into important environmental factors driving the distribution of
90 individual targets, which may, in turn, improve PFT parameterization in DGVMs.

91 Comparative studies that evaluate the present-day PFT distributions of DGVMs in a systematic manner, with
92 reference to a field-based evaluation dataset are, with some exceptions (Druel et al., 2017), few. In this study, we
93 evaluate vegetation distribution, translated to PFT profiles, obtained by three different methods (DGVM, RS, DM)
94 and use an independently collected field-based dataset of vegetation distribution, AR (the Norwegian National
95 map series for Area Resources), for the evaluation. Furthermore, we explore if environmental correlates of
96 vegetation-type distributions identified by DM can be used to improve DGVMs by adjusting parameter settings
97 for high-latitude PFTs.

98 To approach these aims, we constructed a conversion scheme to harmonize the classification schemes of RS, DM
99 and AR into the PFTs used by the DGVM. We represent the present-day vegetation coverage by using plant
100 functional type profiles (PFT profiles), vectors of relative abundances of PFTs within an area, e.g. a given study
101 plot, summing to one. We then compare the PFT profiles obtained by DGVM, RS and DM with the AR reference
102 on 20 selected study plots across the Norwegian mainland. Finally, we conduct a series of sensitivity experiments
103 (ref. chapter 4) which build upon the results of the analyses performed in this study to explore if the DGVM
104 performance can be improved by adjusting DGVM parameters for selected environmental drivers identified by
105 DM.

106 **2 Methods**

107 **2.1 Study area – Norway**

108 The study area covers mainland Norway, spanning latitudes from 57°57'N to 71°11'N and longitudes from 4°29'E
109 to 31°10'E. Norway is characterized by a gradient from a rugged terrain with deep valleys and fjords in the western,
110 oceanic parts to gently undulating hills and shallow valleys in the central and eastern, more continental parts.
111 Temperature and precipitation show considerable variation with latitude, distance from the coast and altitude
112 (Førland, 1979). While the mean annual precipitation ranges from 278 mm in the central inland of S Norway to
113 more than 5000 mm in mid-fjord regions along the western coast, the yearly mean temperature ranges from 7°C
114 in the southwestern lowlands to -4°C in the high mountains (Hanssen-Bauer et al., 2017).

115 The vegetation of Norway is structured along two main bioclimatic gradients (Fig. 1); one related to
116 temperature/growing-season length and one to humidity/oceanicity (Bakkestuen et al., 2008). Broadleaf deciduous
117 forests, regularly found in the southern and southwestern parts (the boreonemoral bioclimatic zone), are further
118 west and north (in the southern boreal zone) restricted to locally warm sites (Moen, 1999). With declining
119 temperatures northwards and towards higher altitudes, evergreen coniferous boreal forests dominate in the
120 southern and middle boreal zones. In the northern boreal zone, the coniferous boreal forests pass gradually into
121 subalpine birch forests, which form the tree line in Norway. A total of about 38% of mainland Norway is covered

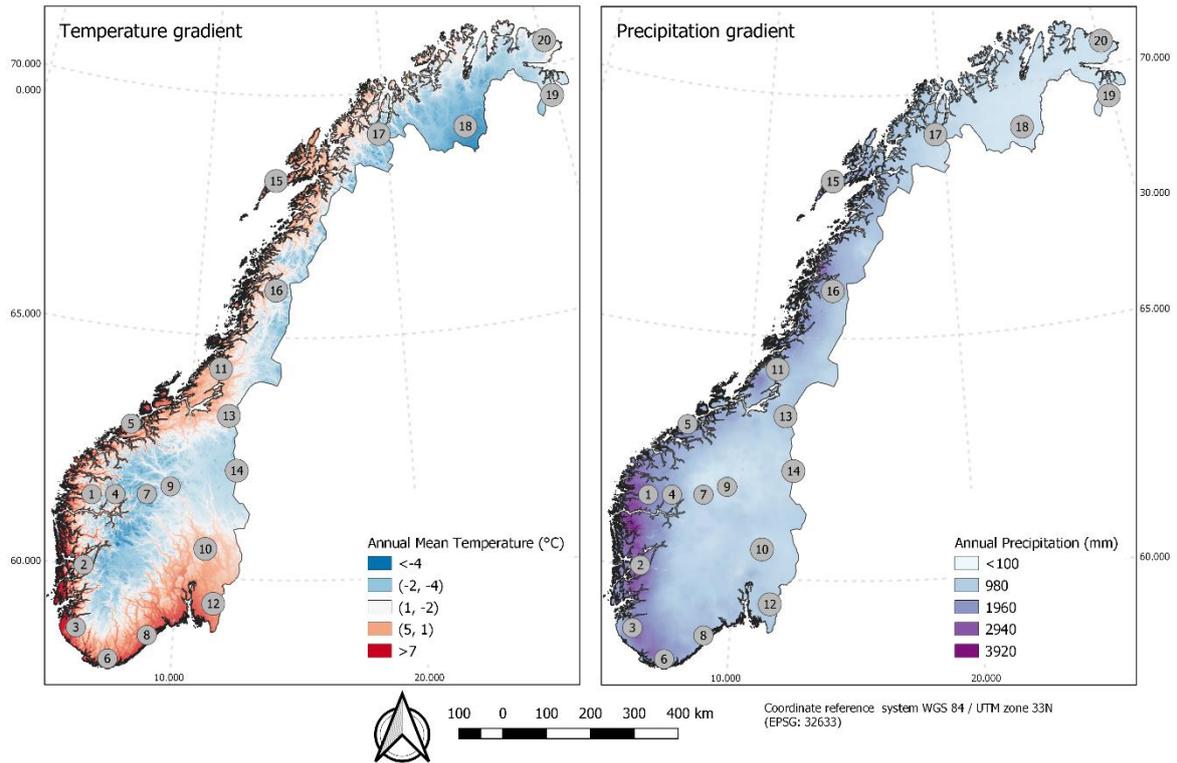
122 by forests, and about 37% of the land is situated above the forest line (of which two thirds is covered by alpine
123 mountain heaths). Wetlands cover approximately 9% and broadleaf deciduous forests about 0.4% of the land area
124 (Bryn et al., 2018).

125 **2.2 The AR reference dataset**

126 Data obtained by in-situ field mapping, which is considered among the most reliable sources of land-cover
127 information (Alexander and Millington, 2000), is practically and economically impossible to obtain in a wall-to-
128 wall format for large land areas such as countries (Ullerud et al., 2020). As an alternative, area-frame surveys
129 based upon stratified statistical sampling may provide accurate, area-representative, homogeneous and unbiased
130 land-cover and land-use data for large areas. To evaluate the three methods for representing vegetation addressed
131 in this study, we used the ‘Norwegian land cover and land resource survey of the outfields’ (*Arealregnskap for*
132 *utmark*) dataset (Strand, 2013), a Norwegian implementation of the mapping program LUCAS (Eurostat, 2003).
133 Data were collected in the period between 2004–2014 in a systematic regular grid covering the whole land area of
134 Norway on which the plots (in total 1081 plots, each 0.6×1.5 km, i.e. 0.9 km²) were placed every 18 km (in latitude)
135 by 18 km (in longitude) (Bryn et al., 2018; Strand, 2013). In each plot, expert field surveyors performed land-
136 cover mapping by use of a system with 57 land-cover and vegetation-type classes (Bryn et al., 2018), mapped at a
137 scale of 1:25 000. The data were provided in vector format with vegetation-type attributes assigned to each mapped
138 polygon.

139 **2.3 Study plots**

140 Twenty out of the 1081 rectangular AR plots were selected to make up our reference dataset, AR (Fig. 1; center
141 coordinates in Table S1). The AR plots spanned elevations from 88 to 1670 m a.s.l., with mean annual temperatures
142 between −4.0°C and 7.1°C and mean annual precipitation between 466 and 2661 mm (Table S1). The gradients of
143 precipitation and temperature are known to be among the most influential for vegetation distribution (e.g., Ahti et
144 al. 1968; Bakkestuen et al. 2008). A series of Kolmogorov-Smirnov tests for comparison of sample mean and
145 variance for these two variables using data from seNorge2 (Lussana et al., 2018a; Lussana et al., 2018b) were
146 obtained to investigate if the 20 selected plots capture the variation across temperature and precipitation in Norway
147 acceptably well compared to the full set of 1081 AR plots (Fig. S2). Additionally, we tested the representativeness
148 across the range of variation for a third variable (precipitation seasonality) which was later selected for sensitivity
149 experiments (see further section 4). While low values of temperature and precipitation are slightly
150 underrepresented in the 20 plots, the total range of variation was well covered. None of the tests for temperature,
151 precipitation and the additional variable (precipitation seasonality) indicate that the sample of the 20 plots deviates
152 from the full set of 1081 plots. The representativeness of the 20 plots was also tested against the full dataset of
153 1081 AR plots with regard to PFT coverage (Supplement S3, Table S3), using a Chi-square test. This test showed
154 that the two datasets are not more dissimilar than expected by chance.



155
 156 **Figure 1 - Locations of the 20 plots across the two main bioclimatic gradients in the study area: temperature (left) and**
 157 **precipitation (right). The plots are numbered by longitude from west to east. Exact values of temperature, precipitation**
 158 **and altitude for each plot are given in Table S1.**

159 **2.4 Methods for representing vegetation**

160 In this study, we use 'plot' as a collective term for two partly overlapping spatial units: (i) the 0.9-km² rectangles
 161 of the AR reference dataset; and (ii) the 1-km² quadrats with the same centerpoint as, and edges parallel to those
 162 of, the AR rectangles. The latter were used for the three methods of DGVM, RS and DM (Fig. S2).

163 Representations of the present-day vegetation for each of these 20 plots were obtained by three different methods:
 164 (i) as the result of single-cell DGVM simulations for each plot; (ii) inferred from an RS vegetation map of the
 165 study area; and (iii) from vegetation-type DM models (Table 1). In order to make the three methods comparable,
 166 vegetation was represented by plant functional type profiles (PFT profiles), obtained by a conversion scheme
 167 (Table S5 and Sect. 2.5). We define a PFT profile as a thematic representation of the land surface in a given plot
 168 or a group of plots, described as a vector of relative PFT abundances, i.e. values that sum up to 1.

169 **Table 1 – Details of each of the methods for representing vegetation. DGVM – dynamic global vegetation model, RS –**
 170 **remote sensing, DM – distribution model. PFT – plant functional type, VT – vegetation type.**

	DGVM	RS	DM
Model type	Process-based mechanistic model	Supervised and unsupervised classification	Statistical model
Software / model name and version	Community Land Model 4.5 – CLM4.5-BGCDV	ENVI (image analysis) and ArcGIS (classification)	R version 3.6.2, generalized linear model
Reference	Oleson et al., 2013	Johansen, 2009	Horvath et al., 2019
Thematic resolution	14 PFTs	25 VTs	31 VTs
Spatial resolution (grid cell)	1 km	30 m	100 m

171

172 2.4.1 The DGVM method

173 The DGVM employed in this study was the CLM4.5BGCDV (hereafter referred to as DGVM), an option provided
174 in NCAR's Community Land Model version 4.5 (CLM4.5) with vegetation dynamics, plant-soil carbon/nitrogen
175 cycle, and multi-layer vertical soil enabled (Oleson et al., 2013). In DGVM, plant photosynthesis, stomatal
176 conductance, carbon/nitrogen allocation, plant phenology and multi-layer soil biogeochemistry are described in
177 accordance with default CLM4.5, while vegetation dynamics (establishment, survival, mortality and light
178 competition) are handled separately based upon simple assumptions of environmental thresholds for establishment,
179 survival and mortality of each PFT (see supplement S6) (Oleson et al., 2013). We used DGVM in the form of
180 single-cell simulations for the 20 plots with grid-cell size set to 1×1 km (Table 1) to simulate the fractional cover
181 of each PFT. All models were run with default CLM4.5 values for surface parameters (e.g. soil texture and depth),
182 with prescribed atmospheric forcing derived from the 3-hourly hindcast of the regional model (SMHI-RCA4)
183 driven by ERA-interim reanalysis for the European Domain of the Coordinated Downscaling Experiment –
184 CORDEX for 1980–2010 (Dyrrdal et al., 2018). The CORDEX model simulation was used because it has a higher
185 spatial resolution than the default atmospheric forcing used in CLM4.5 (0.11°×0.11° and 0.5°×0.5°, respectively).
186 An inspection of the choice of atmospheric forcing, by which the CORDEX data were compared with the SeNorge
187 data used for DM, showed minimal differences (Fig. S5). Only results obtained using CORDEX data are therefore
188 shown in this paper. The 30-year CORDEX data was cycled during the spin-up. A 30-year period is consistent
189 with WMO climatological normal based on the rationale that a 30 year-period is short enough to avoid large long-
190 term trends while long enough to include the range of variability. Thus, the data are not de-trended or averaged.
191 The model was run with default PFT parameters (Table S7). All the selected sites are mostly undisturbed. In our
192 experiments, soil C and N were firstly initialized using a restart file from an existing global present-day spin-up
193 simulation with prescribed vegetation. Each model simulation was spun-up for 400 years to establish a vegetation
194 in equilibrium with the current climate after initialization from bare ground. In three plots where the equilibrium
195 of vegetation was questionable (plot 6, 12 and 17), we extended the spin-up by 400, 200 and 200 years respectively
196 to check if any effect on PFT profile could be seen. No significant changes in the PFT profile was noted in these
197 three instances (Fig. S11.1 and Fig. S11.2) and therefore we kept the initial 400 year spin up for all the sites. A
198 20-year average at the end of the spin-up was used as input for calculation of PFT profiles (representing years
199 1990–2010), which corresponds with the data-collection timeframe of DM, RS and AR.

200 Among the 15 PFTs used in CLM4.5 to represent vegetated surfaces globally (Lawrence and Chase, 2007), only
201 six (plus bare ground) were relevant for our study area (Table S5). Bare ground was predicted to occur where plant
202 productivity was below a threshold value (Dallmeyer et al., 2019). The DGVM simulates the vegetated land unit
203 only (non-grey boxes in Fig. S8), while other land units within the 20 plots, including glaciers, wetlands, lakes,
204 cultivated land and urban areas, make up the “EXCL” PFT category (Table S5). The percentage cover fraction of
205 each PFT is equal to the average individual's fraction projective cover (FPC_{ind}) multiplied by the number of
206 individuals (N_{ind}) and average individual's crown area ($CROWN_{ind}$). FPC_{ind} is a function of the maximum leaf
207 carbon achieved in one year, while $CROWN_{ind}$ is related to dead stem carbon simulated by the model. N_{ind} is
208 mainly determined by establishment and survival rate controlled by establishment and survival threshold
209 conditions (Levis et al., 2004). We obtained PFT profiles for each plot by excluding the EXCL category and
210 recalculated fractions of the vegetated land unit covered by each PFT to sum up to one.

211 **2.4.2 The RS method**

212 As RS product we used SatVeg (Johansen, 2009), a vegetation map for Norway with 25 land-cover classes and a
213 spatial resolution (grid cell size) of 30 m (Table 1). SatVeg is obtained by a combination of unsupervised and
214 supervised classification methods, applied to Landsat 5/TM and Landsat 7/ETM+ images within the near-infrared
215 and mid-infrared spectrum covering the period 1999–2006. While with the supervised classification, training data
216 is based on well-labelled data from the study area, during the unsupervised classification the algorithm is only
217 supplied with the number of output classes without further interference of the user. Only grid cells that were within
218 each 1-km² plot with a majority of their area were taken into consideration for further calculations.

219 **2.4.3 The DM method**

220 The distribution models (DMs) for 31 vegetation types (VT) obtained by Horvath et al. (2019) using generalized
221 linear models (GLMs, with logit link and binomial errors, i.e. logistic regression), were used for this study. The
222 VT data were collected during years 2004–2014. The DMs were obtained by using wall-to-wall data for 116
223 environmental predictors from six groups (topographic, geological, proximity, climatic, snow and land cover),
224 gridded to a spatial resolution of 100×100 m (Table 1) as predictors. Important predictors were selected by an
225 automated stepwise forward-selection procedure for each of the 31 VTs individually, thus each final model is built
226 upon only a narrow selection of important predictors (Horvath et al., 2019 supplement S7). All DMs were
227 evaluated using an independent evaluation dataset and by calculating the area under the receiver operator curve
228 (AUC), a threshold-independent measure of model performance commonly used in DM. (see Horvath et al., 2019
229 for details). AUC can be interpreted as the probability that the model predicts a higher suitability value for a
230 random presence grid cell than for a random absence grid cell (Fielding and Bell, 1997). A seamless vegetation
231 map (i.e. with one predicted VT for each grid cell with no overlap and no gaps) was obtained from the stack of 31
232 probability surfaces by assigning to each grid cell the VT with the highest predicted probability of occurrence
233 within that cell (Ferrier et al., 2002). Grid cells with the majority of their area within a 1-km² plot were used for
234 further calculations (Fig. S6).

235 **2.5 Conversion to PFT profiles**

236 Harmonisation of the various vegetation classification systems was accomplished by a conversion scheme that
237 represented each grid cell (RS and DM) or polygon (AR) in each of the 20 plots with one out of the six PFTs
238 recognised by DGVM (Table S5 and Fig. S6). The scheme was obtained by expert judgements and solicited by a
239 consensus process which involved ecologists participating in the AR18x18 survey as well as scientists working
240 with RS and DGVMs.

241 We used the conversion scheme of Table S5 to generate wall-to-wall PFT maps from the original RS, DM and AR
242 datasets (Table 1) by assigning one PFT to each 30×30 m grid cell, 100×100 m grid cell or VT polygon,
243 respectively. PFT profiles for each plot, at the same thematic resolution as for DGVM, were obtained as the vector
244 with fractions of grid cells or polygons assigned to each of the six PFTs. ‘EXCL’ classes not represented in DGVM
245 (cf. Table S5) were left out to minimise the effect of land use, which could otherwise have brought about
246 differences in PFT profiles among the compared methods. PFT profiles were obtained for each combination of
247 method and plot. To test for deviations in PFT coverage between the methods across the whole study area,
248 aggregated PFT profiles were obtained by averaging the 20 PFT profiles obtained for each method.

249 2.6 Comparison of PFT profiles

250 To examine the overall pattern across the study area and to assess the models' ability to produce overall predictions
251 of PFTs that accord with the PFTs' overall frequency (as given by the reference) aggregated PFT profiles obtained
252 by each of the DGVM, RS and DM methods were compared with the aggregated PFT profile of the AR reference
253 dataset by a chi-square test (Zuur et al., 2007). To identify strongly deviating modelling results at a plot scale, the
254 dissimilarity between PFTs profiles obtained by each of the DGVM, RS and DM methods and the PFT profile of
255 the AR dataset for each plot was calculated by using proportional dissimilarity (Czekanowski, 1909):

$$256 \quad d_{hj} = \frac{\sum |y_{hji} - y_{0ji}|}{\sum (y_{hji} + y_{0ji})} = 1 - \frac{2 \sum \min(y_{hji}, y_{0ji})}{\sum (y_{hji} + y_{0ji})}$$

257 where y_{hji} refers to the specific element in a PFT profile vector (the fraction occupied by the PFT in question) given
258 by method h (DGVM, RS or DM; $h = 1, \dots, 3$; the value $h = 0$ refers to the AR reference dataset), j refers to
259 sampling unit ($j = 1, \dots, 20$) and i refers to PFT ($i = 1, \dots, 6$). Proportional dissimilarity is the Manhattan measure
260 standardized by division by the sum of the pairwise sums of variable values (here PFTs). Since the values of each
261 PFT profile sums to one, the index reduces to

$$262 \quad d_{hj} = 1 - \sum \min(y_{hji}, y_{0ji})$$

263 The proportional dissimilarity index is appropriate for incidence data like PFT abundances, i.e. variables that take
264 zero or positive values. The index reaches a maximum value of 1 when two objects have no common presences
265 (here, PFTs present in both compared objects) and ignore joint absences (zeros). To assess the degree to which the
266 models produce pairwise similar differences, we compared the pairwise differences between the proportional
267 dissimilarity values among methods, using a Wilcoxon-Mann-Whitney paired samples test.

268 All raster and vector operations related to DM, RS and AR were carried out in R (version 3.4.3) (R Core Team,
269 2019) using packages "rgdal" (Rowlingson, 2019), "raster" (Hijmans, 2019) and "sp" (Pebesma and Bivand,
270 2005), while graphics are produced using the "ggplot2" package (Wickham, 2016). Statistical analyses were
271 carried out in R (version 3.4.3), using the "vegan" package (Oksanen et al., 2019). All maps were produced in
272 QGIS (QGIS Development Team, 2019).

273 3 Results

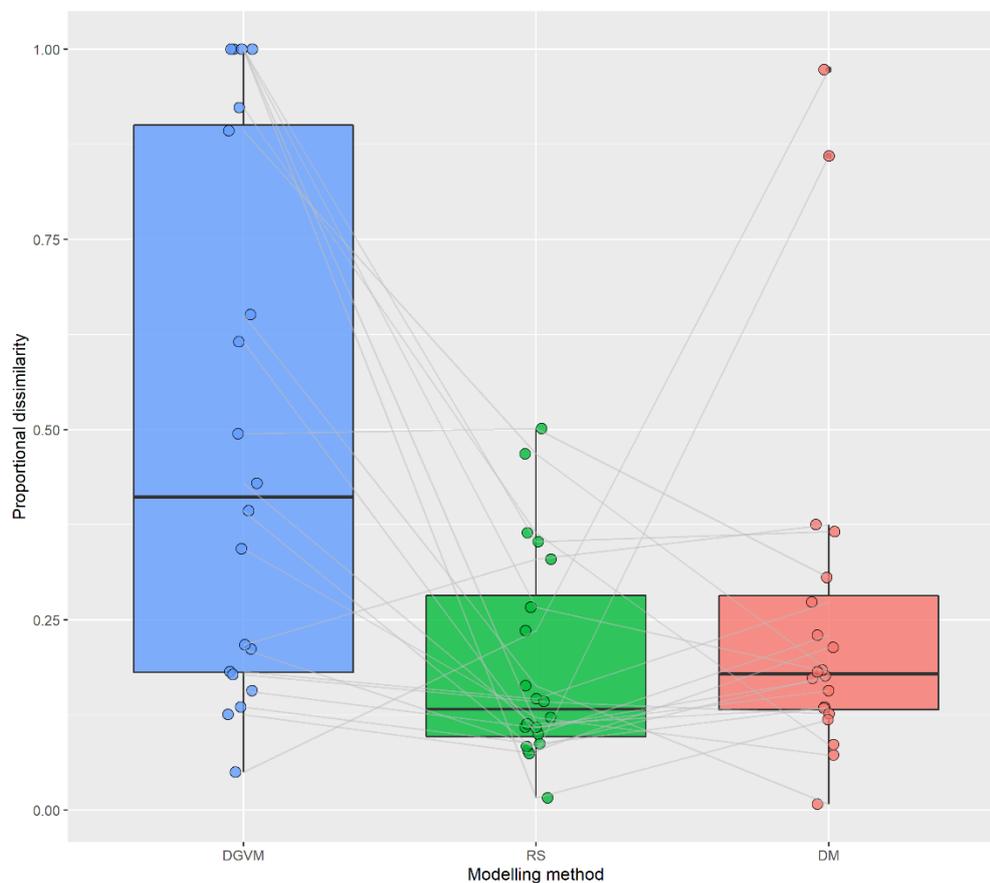
274 The aggregated PFT profiles for the RS and DM datasets did not differ significantly from those of the reference
275 AR dataset according to the chi-square test, while a significant difference was found for the DGVM profiles (Table
276 2). While the proportion of grid cells attributed to the PFT boreal NET by the RS and DM methods underestimated
277 AR values by 3.0 and 2.8 percentage points, respectively, DGVM overestimated the proportion of boreal NET by
278 20.4 percentage points compared to the AR reference. Also, unproductive areas (BG) were overestimated by
279 DGVM (by 16.6 percentage points), less so by RS (4.0 percentage points), while this PFT was slightly
280 underrepresented by DM (by 5.0 percentage points). Discrepancies were also observed for the cover of the C3
281 PFT, which was overestimated by RS and DM (by 7.2 and 2.9 percentage points, respectively) and underestimated
282 by DGVM (by 3.0 percentage points). Furthermore, DGVM overestimated BG and temperate BDT cover on the
283 expense of boreal BDT and boreal BDS.

284 **Table 2 - PFT profiles (columns) aggregated across all 20 plots for the three methods compared in this study and the**
285 **AR reference dataset. Results of comparisons of aggregated PFT profiles for each of the three methods with the**

286 reference are also given. DGVM – dynamic global vegetation model, RS – remote sensing, DM – distribution model, AR
 287 – reference dataset. BG – bare ground, boreal NET – boreal needleleaf evergreen trees, temperate BDT – temperate
 288 broadleaf deciduous trees, boreal BDT – boreal broadleaf deciduous trees; boreal BDS - boreal broadleaf deciduous
 289 shrubs, C3 – C3 grasses.

PFT	Compared methods			Reference
	DGVM (%)	RS (%)	DM (%)	AR (%)
BG	29.5	17.0	7.9	12.9
Boreal NET	57.2	34.0	33.8	36.8
Temperate BDT	5.6	2.0	0.2	0.5
Boreal BDT	3.1	12.5	17.2	15.5
Boreal BDS	4.1	23.8	34.5	30.8
C3	0.5	10.7	6.4	3.5
Chi-square test	$\chi^2= 45.98$, df = 5, p < 0.05	$\chi^2= 6.36$, df = 5, p = 0.27	$\chi^2= 2.61$, df = 5, p = 0.75	

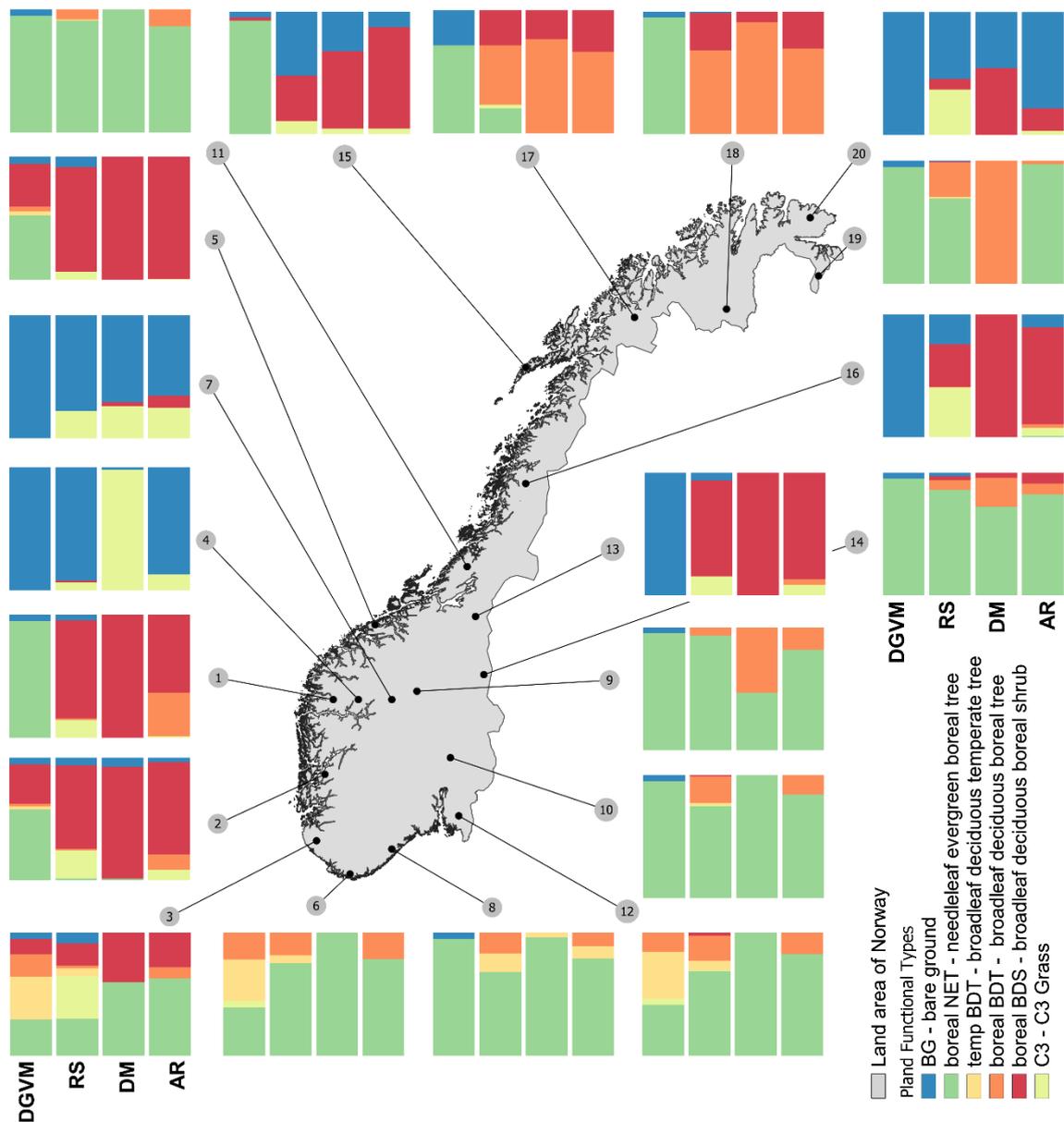
290
 291 In accordance with results from comparisons between aggregated PFT profiles obtained by the three methods and
 292 those obtained for the reference dataset, DGVM profiles for individual plots were significantly more dissimilar to
 293 the AR reference than RS and DM profiles (Fig. 2). While RS had the lowest median proportional dissimilarity
 294 with the AR reference (0.19, compared to 0.26 for DM and 0.41 for DGVM), DM had the lowest spread of
 295 dissimilarity values, measured as interquartile difference (0.12, compared to 0.19 for RS and 0.72 for DGVM),
 296 among the three methods (Fig. 2). While no dissimilarity value for RS was above 0.50, two plots (4, 19) acted as
 297 strong outliers in the distribution of DM values (cf. Fig. 2). Additionally, a comparison of proportional dissimilarity
 298 between pairs of methods revealed significant differences between DGVM profiles and those obtained by RS and
 299 DM (Wilcoxon rank-sum tests: W = 111, p = 0.0167; and W = 88, p = 0.0026, respectively), while RS and DM
 300 profiles were not significantly different from each other (Wilcoxon rank-sum test: W = 161, p = 0.3013).



301

302 **Figure 2 - Proportional dissimilarity values between PFT profiles for each combination of 20 plots and each of the three**
 303 **methods compared in this study, and the corresponding plot in the AR reference dataset. The thick horizontal line, the**
 304 **box and the whiskers represent the median, the interquartile difference and the range of values for each method.**

305 Visual inspection of spatial patterns of PFT profile characteristics across the 20 plots suggests that the best
 306 agreement among the methods was obtained for the south-eastern part of the study area, dominated by the boreal
 307 NET (Fig. 3 and Table S10). Compared to the AR reference dataset, PFT profiles obtained by DGVM were
 308 strongly biased: in the north (plots 17 and 18) towards boreal NET on the cost of boreal BDS, near the west coast
 309 (plots 1, 2, 5 and 15) towards boreal NET on the cost of boreal BDS, and in southern coastal areas (plots 3, 6 and
 310 12) towards temperate BDT instead of boreal NET. In plots 13 and 16 DGVM failed to establish vegetation
 311 (predicting bare ground) where AR reported boreal BDS. RS represented the PFT profiles of the AR reference
 312 well in most cases, but tended to overestimate the frequency of dominance by C3 grasses at several locations (plots
 313 3, 16 and 20). While DM showed no general spatial pattern of PFT profile deviations from the reference dataset,
 314 PFT profiles of plots 4 and 19 obtained by DM had almost no similarity to the corresponding profiles of the AR
 315 reference dataset: C3 grasses and boreal BDT were predicted instead of bare ground and boreal NET, respectively.



316

317 **Figure 3 – PFT profiles for each of the 20 plots for the three methods compared in this study and the AR reference**
 318 **dataset. The columns in each cluster of four bar-charts represent, from left to right, the methods dynamic global**
 319 **vegetation model (DGVM), remote sensing (RS) and distribution model (DM), with the AR reference dataset to the**
 320 **right.**

321 **4 Sensitivity experiments and model improvement**

322 We used the results of PFT profile comparisons between DGVM and the AR reference (Fig. 3) and the results
 323 obtained for the DM dataset as a starting point for exploring the possible causes of the poor performance of DGVM.
 324 We first identified the three most abundant PFTs (i.e. boreal NET, boreal BDT and boreal BDS) in our set of plots
 325 (Table S3). Thereafter, we identified the major VTs predicted by DM in those plots that were translated into these
 326 PFTs using the conversion scheme (Table S5) (pine forest, birch forest and dwarf shrub heath, respectively; Table
 327 3). Based on the results from Horvath et al. (2019), the corresponding final models for these three VTs were
 328 examined to identify important environmental variables that were driving the distribution of the VTs but not
 329 represented in DGVM. We recognized three environmental predictors that are critical for the distribution of each
 330 of these VTs and exhibit a clear threshold signature in the frequency-of-presence plots (i.e. graphs showing
 331 variation in the abundance of the VT as a function of an environmental predictors, also see Fig. S12): snow water
 332 equivalent in October (swe_10), minimum temperature in May (tmin_5) and precipitation seasonality
 333 (bioclim_15). Precipitation seasonality is defined as the ratio of the standard deviation of the monthly total
 334 precipitation to the mean monthly total precipitation (i.e. the coefficient of variation), expressed as percentage
 335 (O'Donnell and Ignizio, 2012). Based on visual inspection of the frequency-of-presence plots, we identified
 336 specific threshold values for each of the three VTs (see Fig. S12 for details) and implemented these threshold
 337 values into DGVM as new limits for establishment of the three PFTs as shown in Table 3. For example, in line
 338 with Fig. S12, VT 2ef and its respective PFT - boreal BDS can only establish when variable swe_10 is less than
 339 380mm.

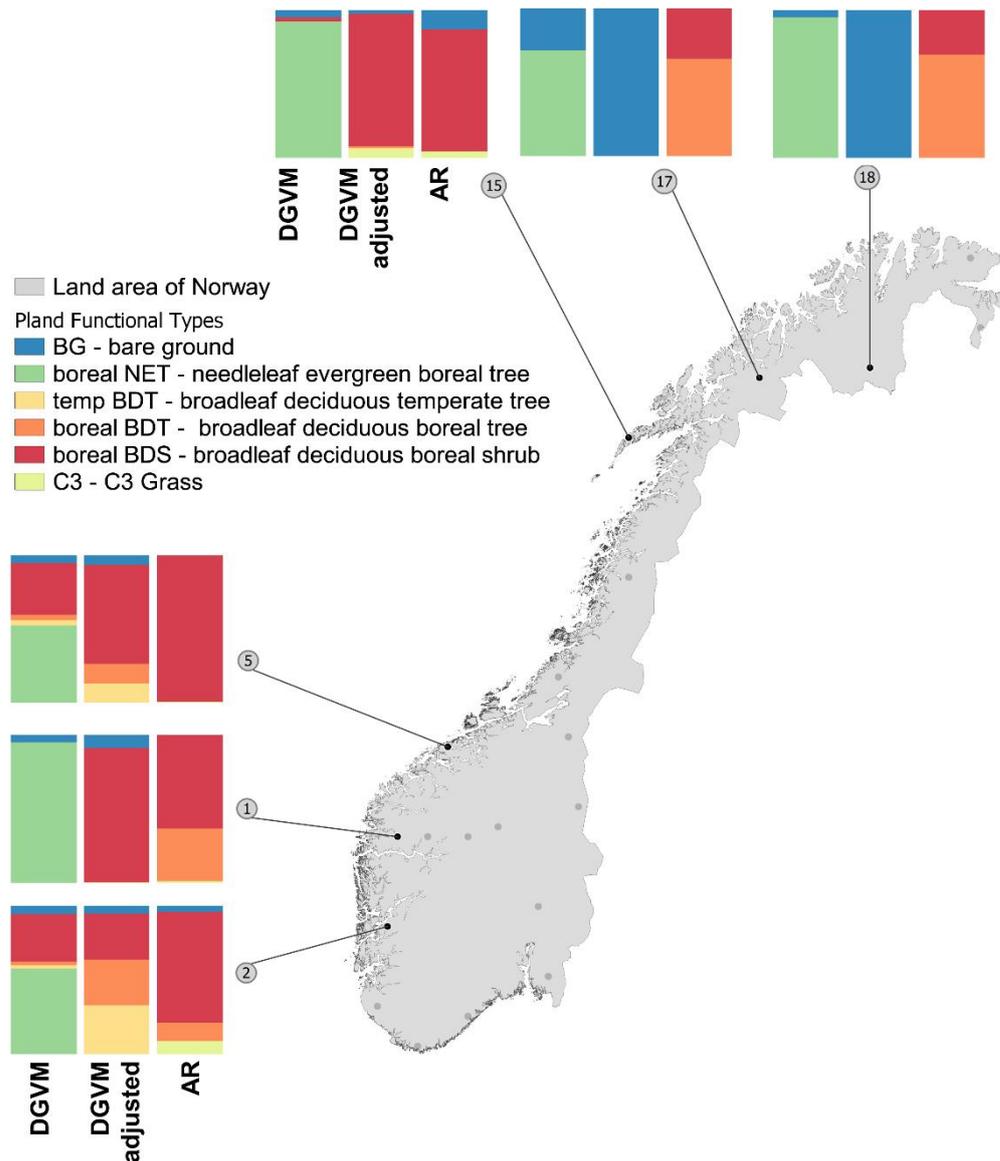
340 We explored the extent to which these additional thresholds improved the performance of DGVM on the subset
 341 of six plots (i.e. 1, 2, 5, 15, 17 and 18) in which the PFT profiles are most biased compared to the AR reference
 342 dataset due to the overrepresentation of the boreal NEB. In total, three sensitivity experiments were carried out by
 343 a stepwise process, in each step a new threshold was added cumulatively to the previous experiment (Table 3).
 344 Namely, in the first sensitivity experiment (i), we added the swe_10 threshold. In the second experiment (ii), we
 345 added both swe_10 and tmin_5 as the threshold. In the last experiment (iii), we added all the three novel thresholds.
 346 Only the results of the third sensitivity experiment with all the three thresholds added are reported here. Results of
 347 the other two experiments are summarised in Table S13.

348 **Table 3 – New thresholds for establishment of the three PFTs explored in DGVM sensitivity experiments. The variables**
 349 **explored were: swe_10 – snow water equivalent in October given in mm; tmin_5 – minimum temperature in May (°C);**
 350 **bioclim_15 – precipitation seasonality (unitless index representing annual trends in precipitation).**

		Sensitivity model run		
		(i)	(ii)	(iii)
VT	PFT	swe_10 (mm)	tmin_5 (°C)	bioclim_ 15
2ef – Dwarf shrub heath / Alpine calluna heath	Boreal broadleaf deciduous shrub	< 380	> -10	–
4a – Lichen and heather birch forest	Boreal broadleaf deciduous tree	< 180	> -7.5	–
6a – Lichen and heather pine forest	Boreal needleleaf evergreen tree	< 150	> -5	< 50

351

352 The results show that while the added thresholds for swe_10 and tmin_5 had little impact on the results (Table
 353 S13), the addition of the threshold for bioclim_15 (i.e., the third sensitivity experiment) largely improved the
 354 performance of the DGVM on the experimental plots explored (Fig. 4). PFT profiles simulated by this experiment
 355 were more similar to those of the AR reference dataset for four out of the six plots in the experimental subset (plot
 356 1, 2, 5 and 15): in plots 1 and 15, Boreal NET was correctly replaced by boreal BDS; in plots 2 and 5 boreal NET
 357 was replaced by boreal BDT, BDS and temperate BDT. Addition of new threshold (bioclim_15) also reduced the
 358 modelled abundance of boreal NET in plots 17 and 18, but DGVM still failed to populate these plots with another
 359 PFT (Fig. 4).



360
 361 **Figure 4 – PFT profiles for the subset of six plots subjected to sensitivity experiments with new DGVM establishment**
 362 **thresholds. The columns in each cluster of three bar-charts represent, from left to right, dynamic global vegetation**
 363 **model (DGVM) with original (default) parameter settings, DGVM with revised parameter settings, and the AR**
 364 **reference dataset. For further details, see Table S13.**

365 5 Discussion

366 5.1 Comparison of PFT profiles

367 The maps of PFT distributions generated by DM and RS are generally similar (Fig. S9) across most of our study
368 area. This indicates that output from DM, which is rarely used for evaluating PFT distributions from DGVMs, can
369 be used for this purpose in addition to the commonly used RS-based datasets. There are, however, some differences
370 between results obtained by the two methods near the northern Norwegian coast and in the mountain areas of
371 western Norway, which will be discussed below in more details.

372 We recognise six possible explanations for the differences in PFT profiles obtained by DGVM, RS and DM for
373 the 20 plots (see Table 5), related to the following issues: (i) the conversion scheme (ref. Table S5); (ii) what is
374 actually modelled by DGVM, RS and DM, e.g. in terms of potential vs actual vegetation; (iii) the performance of
375 individual DM models; (iv) transforming predictions from single DMs into a seamless vegetation map, i.e. that
376 assigns one VT to each grid cell; (v) DGVM performance; and (vi) missing PFTs in DGVM.

377 5.1.1 The conversion scheme

378 The conversion schemes used to reclassify vegetation and land cover classes into PFTs have been reported as a
379 possible contributor to erroneous PFT distributions (Hartley et al., 2017). While we use a simple conversion scheme
380 that assigns each land cover type/vegetation type to one and only one PFT (Dallmeyer et al., 2019), more complex
381 conversion schemes exist, by which each land cover class is translated into a multi-PFT composition that co-occur
382 within a grid cell (Bonan et al., 2002; Li et al., 2016; Poulter et al., 2011; Poulter et al., 2015). Our approach may
383 be advantageous when the classes to be converted are homogeneous, in the sense that one PFT is clearly
384 dominating in the type, and in the sense that the range of variation within the class in PFTs is negligible, such as
385 is the case for 90% of the DM- and RS-classes in our study. Our simple scheme may, on the other hand, be a source
386 of uncertainty when quantitatively important VTs are ambiguous in one way or the other, or, more commonly, in
387 both ways at the same time. The set of VTs used in our study includes several relevant examples: VTs that may
388 include a wide spectrum of tree-dominant types; the VT '*1a/1b - Moss snowbed / Sedge and grass snowbed*',
389 which covers a range of variation in the relative abundance of graminoids and, hence, shows affinity to C3 as well
390 as to BG; and the VT '*8a - Damp forest*', which is usually dominated by the evergreen Scots pine and converted
391 into boreal NET, but that in some instances (e.g. after clear-cutting) is dominated by deciduous trees like *Betula*
392 spp. and should then be converted into boreal BDT (Bryn et al., 2018). However, a close inspection of DM shows
393 that our method reproduced similar PFT profiles as the reference dataset for all plots, except two out of 20 plots
394 (the two outliers on Fig. 2, plots 4 and 19 in Fig. 3).

395 In our case, a more complicated conversion scheme is likely to be compensated for by the sub-grid complexity
396 introduced in the process by which PFT profiles are obtained. Rather than estimating a PFT profile for the 1-km²
397 plot directly, i.e. in one operation as in DGVM, the RS-based classes and VTs are first converted into PFTs in their
398 original resolution, and then subsequently subjected to aggregation to obtain the PFT profiles. This results in a
399 sub-grid PFT heterogeneity that could otherwise be implemented by using a more complex conversion scheme.

400 5.1.2 What is modelled by DGVM, RS and DM

401 The methods used in this study produce different representations of the vegetated land surface in terms of actual
402 or potential natural vegetation (Table 4). In order to model future vegetation changes and feedbacks, functional

403 type-based models like DGVM implicitly address the processes that control the distribution of vegetation (Bonan
404 et al., 2003; Song et al., 2013). Simulating natural vegetation processes under a given climatic equilibrium scenario
405 (at any given time), DGVM produces a model of potential natural vegetation (ex. Bohn et al., 2000, Hengl et al.
406 2018). RS-based classifications, on the other hand, describe the land surface at a specific time-point or changes
407 through time (e.g. Arctic greening and browning) (Myers-Smith et al., 2020) and, accordingly, portrays actual
408 vegetation as influenced by previous and ongoing land use (Bryn et al., 2013). Depending on the modelling setup,
409 DM may pragmatically describe the current ecological envelope of a target or aim at revealing the proximate
410 causes for its distribution (Ferrier and Guisan, 2006), thus modelling either actual or potential natural vegetation,
411 depending on the input data used for modelling (Hemsing and Bryn, 2012; Hengl et al., 2018).
412 In this study, we carefully restricted our attention to PFTs that represent natural vegetation, excluding VTs with
413 strong anthropogenic influences. This was done for all methods and the AR reference. Nevertheless, differences
414 with respect to what is actually modelled by the different methods, potential vegetation by DGVM and actual
415 vegetation by RS and DM, may have contributed to the observed among-model differences in PFT profiles.

416 **5.1.3 DM performance**

417 While the performance of the DM method is overall good, distribution models of individual VTs vary in
418 performance (with AUC values ranging from 0.671 to 0.989) according to the study by Horvath et al. (2019).
419 Several reasons for the low predictive performance of some DM are identified, of which the most important is
420 considered to be important predictors missing in the training data. This might seem counter-intuitive, given the
421 large number of predictor variables used in the study (n=116). However, the authors conclude that several
422 important factors for the distribution of vegetation are not at all represented in the dataset (e.g. NDVI, LiDAR
423 etc.), among others because they are almost impossible to obtain data for with required spatial resolution (e.g. soil
424 nutrients). The DM method requires estimates for the probabilities of occurrence for (almost) all individual
425 vegetation types to create a seamless vegetation map, which in turn is required for making estimates for the PFT
426 profiles as robust as possible. Thus, in this context, ‘poor’ models are better than no model.

427 Individual models’ performance might be the reason for the two plots whose PFT profiles deviate strongly from
428 the AR reference (Fig. 2 and Fig. 3). For plot 4, the discrepancy is due to VT “*1a/1b - Moss snowbed / Sedge and
429 grass snowbed*”, which is represented by one of the best performing among the 31 DMs. For this VT, conversion
430 scheme bias is a more likely reason for the deviant PFT profile. For plot 19, boreal BDT is modelled because the
431 VT predicted by DM is “*4a – Lichen and heather birch forest*”. The fact that the DM for this VT is among the
432 inferior DMs (see the ranking of individual models presented in Horvath et al. (2019)) makes this explanation
433 more likely in this case.

434 **5.1.4 Transformation of single-DM predictions into a vegetation map**

435 The performance of DM on the particular plots may also be influenced by the method chosen for transforming
436 predictions from one DM for each VT into a seamless vegetation map. Assigning to each grid cell the VT with the
437 highest predicted probability of presence in that cell, which is a commonly used method for this purpose (Ferrier
438 and Guisan, 2006), favours VTs represented by good DMs. This is brought about by good DMs having a
439 distribution of predictions that is more spread out (with larger predictions for the grid cells identified as the most
440 favourable cells) than poor DMs (Halvorsen, 2012). However, since the probability of presence for each VT was

441 predicted separately for each grid cell, the probability values for every VT vary independently of the probabilities
 442 for the other VTs, throughout the study area. Thus, we regard the chance that one VT consistently outperforms
 443 another VT over all the grid cells to be negligible. Alternative methods for this purpose should be tested in the
 444 context of DGVM evaluation. To avoid uncertainties associated with conversion between type systems and
 445 perhaps even further improve the performance of DM, we recommend exploring the option of using PFTs directly
 446 as targets in DM. Direct modelling of PFTs rather than taking the detour via VT models may reduce the number
 447 of environment predictors required (116 layers used in Horvath et al. (2019)) in addition to circumventing the
 448 complicated process of modelling thematically narrow vegetation types (VTs). Another potential advantage of
 449 modelling PFT targets directly is that the model parameters will then be PFT specific, and not in need of being
 450 converted (from VT into PFT).

451 To further reduce the biases and uncertainties of DM-based PFT profiles, we recommend exploring the use of
 452 variables derived from RS directly as predictors in DM. Previous studies have shown that RS -based predictors
 453 may enhance DM performance on different scales: on vegetation-type level (Álvarez-Martínez et al., 2018); on
 454 the habitat-type level (Mücher et al., 2009); and on the PFT level (Assal et al., 2015). Further suggestions for
 455 improvement of the methods used in this study are found in Table 4.

456 **Table 4 – A summary of the key properties of the three methods compared in this study. DGVM – dynamic global**
 457 **vegetation model, RS – remote sensing and DM – distribution model.**

Key property	Method		
	DGVM	RS	DM
Modelled property	Process-based vegetation model – using <i>a priori</i> parameterizations	Classification based on satellite imagery (spectral reflectance)	Statistically based model of a target (response) and the environment (predictors)
Main purpose	Feeding vegetation changes into ESM for further quantification of feedbacks between land surface and the atmosphere	Mapping of land cover or land use for descriptive purposes, management or monitoring	Predicting the spatial distribution of a target and/or to summarise its relationship with the environment
Material	Climate forcing, PFT parameters, host model	Satellite imagery in different bands	Presence-absence training data, environmental predictors
Spatial extent	Global to regional (Single-cell tests)	Global to local	Regional to local
Modelling outcome	Potential vegetation	Actual vegetation	Potential or actual vegetation, depending on the training data
Advantages	<ul style="list-style-type: none"> – Addresses the processes – Feedback loops with other Earth system components can be included – Continuous temporal scale of prediction into the future 	<ul style="list-style-type: none"> – Observation-based – High spatial resolution – Good temporal coverage 	<ul style="list-style-type: none"> – Opens for use of proxies for important predictors – May provide insight into drivers of distributions
Disadvantages	<ul style="list-style-type: none"> – Low performance (e.g. compared with RS and DM) as long as the underlying processes are not fully understood and properly parameterised – Parameter intensive – Resource demanding 	<ul style="list-style-type: none"> – Data are sensitive to cloud cover and shaded areas – Atmospheric correction needed – Provides limited insight to the processes that regulate the distributions of land cover types – No feedback included 	<ul style="list-style-type: none"> – Provides limited insight to the processes that regulate the distributions of targets – Temporally static (one time-point addressed by each model) - No feedback included
Possible interactions with the other methods	<ul style="list-style-type: none"> – May improve DM by pointing at relevant predictor variables – May improve RS by identifying threshold values 	<ul style="list-style-type: none"> – May improve DGVM by improved parameterization (based on RS indices) – May improve DM by providing predictor variables, directly or as indices (NDVI, etc) 	<ul style="list-style-type: none"> – May improve parameterization and envelope discrimination of DGVM – May improve RS by targeting specific PFTs that have similar reflectance, but different ecology

458

459 5.1.5 DGVM performance

460 Our results show that, for many plots, the PFT profiles simulated by DGVM differ from those of the AR reference
461 dataset. According to our results, DGVM overestimates the coverage of bare ground and boreal NET and
462 underpredicts the cover of C3 grasses, boreal BDT and boreal BDS. While the AR reference dataset shows that
463 the northern plots (specifically plots 17 and 18) are covered by mountain birch forest and shrubs (boreal BDT and
464 boreal BDS), DGVM predicts dominance of boreal NET in these plots. Overestimation of boreal NET has also
465 been reported by Hickler et al. (2012) for large parts of Scandinavia, who attributed this to the lacking
466 representation of shade tolerance classes in DGVM models. A similar pattern is seen in our results: the PFT profiles
467 obtained by DGVM during the 400-year spin-up (Fig. S11) show no sign of boreal BDT in the early phases of
468 model prediction, as would be expected of an early successional forest in Norway.

469 Our results further suggest that the DGVM underrepresents grasses and shrubs compared to the reference dataset.
470 This may be explained by the built-in constraints in the light competition scheme of DGVM. The model assumes
471 that regardless of grass and shrub productivity, trees will cover up to 95% of the land unit when their productivity
472 permits (Oleson et al., 2013). The priority given to a PFT in DGVM decreases with the stature of the organisms in
473 question because of the increasing probability that a lower layer is covered by another layer. The degree of
474 underrepresentation is therefore expected to increase from shrubs to grasses. Accordingly, DGVM predicts
475 dominance by trees in the most productive regions, by grasses in less productive regions, and by shrubs in the least
476 productive non-desert regions (Zeng et al., 2008). The underrepresentation of C3 grasses by DGVM across the 20
477 plots accords with the results of Zhu et al. (2018), who found that C3 grasses are underpredicted on a global level
478 in an earlier version of DGVM.

479 Inappropriate parameterisation of shrubs may be a reason why the DGVM underestimates boreal BDS in many of
480 the coastal plots (1, 2, 5, 15) (Table S6). The implementation of shrubs as a new PFT in an earlier version of
481 DGVM (CLM3-DGVM) by Zeng et al. (2008), parameterised for representation of taller shrubs with heights
482 between 0.1 and 0.5 m, may not suit the majority of dwarf shrubs (of genera *Calluna*, *Betula*, *Empetrum*) that
483 abundantly occurs in Norwegian ecosystems. To this, Castillo et al. (2012) add that the sparse shrub and grass
484 vegetation cover simulated by DGVM in the tundra regions may be caused by the soil moisture bias inherited from
485 the host land model CLM4 (Lawrence et al., 2011). Another reason for DGVM's underestimation of boreal BDS
486 in coastal areas could be the 4000-yr tradition of coastal heath management in Norway (Bryn et al., 2010) which
487 causes a large discrepancy between the actual vegetation modelled by RS, DM and AR and the potential natural
488 vegetation simulated by DGVM under present-day climatic conditions (e.g. Bohn et al., 2000, Hengl et al. 2018).
489 We therefore argue that more sensitivity studies of PFT-specific parameters for height, survival, establishment
490 etc., across all PFTs, are needed.

491 Some discrepancies in the DGVM output might be caused by the climate forcing used in the simulations, looped
492 for the period 1980–2010. Long-term historical climate effects on vegetation distribution were not included in our
493 model simulation. However, we noticed that vegetation distribution was insensitive to interannual variation or
494 decadal variation of the climate forcing when it reached equilibrium state in most of our study sites. Even though
495 long-term historical climate effects (such as cooler temperature in the early 20th century) may favour boreal BDS
496 rather than boreal NET, we consider such historical effects to have only minor impact on the already large biases
497 observed in DGVM (e.g., too much boreal NET and too few BDS). We also note that DGVM used a spatially
498 coarser CORDEX reanalysis (11x11 km) to supply high temporal resolution (6-hourly) atmospheric forcing data,

499 while the climate predictors used in DM was derived from observation-based SeNorge2 dataset with 1x1 km spatial
500 resolution and daily temporal resolution. The larger biases in CORDEX reanalysis data may also contribute to the
501 large mismatch between DGVM and the reference dataset. We have compared the average annual temperature and
502 annual precipitation of the two input datasets used in DGVM and DM to look for differences (see Fig. S4). It
503 appears that precipitation estimates by CORDEX for the 20 plots were slightly higher than SeNorge estimates, the
504 converse (but less strongly) was true for temperature. The consequences of these differences in the input data
505 might be investigated in follow-up studies.

506 Despite the shortcomings discussed above, DGVM performs reasonably well for some PFTs. One example is the
507 temperate BDT, which is correctly predicted by the model to be restricted to the southern coastal plots (Bohn et
508 al., 2000; Moen, 1999). This finding suggests that some climatically driven PFTs (i.e. temperate BDT) are well
509 implemented by the existing parameters in the DGVM used in this study.

510 **5.1.6 Missing PFTs**

511 DGVM coerces the World's immense variation in plant species composition (vegetation) into a very limited
512 number of predefined PFTs, compared to classification schemes used by the other methods in this study (RS, DM
513 and AR; see Table S5) and by other approaches to systematisation of ecodiversity (e.g. Dinerstein et al., 2017;
514 Keith et al., 2020). In particular, the number of high-latitude specific PFTs is insufficient to realistically represent
515 the biodiversity of these ecoregions, as pointed out by Bjordal (2018) and Vowles & Björk (2017). Comparisons
516 between PFT profiles obtained by DGVM and profiles obtained by DM suggest specific vegetation types that need
517 to be better represented in DGVMs, either by improving an existing PFT or by adding a new PFT (e.g. dwarf
518 shrubs vs. tall shrubs; moss dominated snow-beds, wetlands, lichens). In our study, the PFT profile of DGVM is
519 represented by the six boreal PFTs, whereas the original data for RS, DM and AR include an average of 17% (ref.
520 Table S3) of the total area that are not represented by these six PFTs (classes for "Excluded" PFT category ref.
521 Table S5). This points to the missing PFTs in the classification scheme of the DGVM, but also to the challenge
522 that certain ecosystems in our study area do not have a representation in the PFT schemes of DGVM. This is
523 exemplified by wetlands; important ecosystems that are still not represented in many of the current DGVMs. This
524 is not only problematic from the perspective of land surface energy balance (Wullschleger et al., 2014), but has
525 also implications for modelling of carbon storage and cycling, and other interactions between the land surface and
526 the atmosphere (Bjordal, 2018).

527 Some recent examples with improvements to the thematic resolution of PFTs in DGVMs are available in the
528 literature (Druel et al., 2019; Coppell et al., 2019; Chadburn et al., 2015; Porada et al., 2016; Druel et al., 2017),
529 and further examples of DGVMs with a larger number of high-latitude PFTs also exist (Euskirchen et al., 2009).
530 In line with these studies, our results demonstrate a great potential for increasing the thematic resolution of
531 DGVMs in general and not limited to the DGVM tested here in terms of developing and parameterizing new
532 specific PFTs to be representative of the high-latitude and high-altitude habitats, and also deriving parameters from
533 observations, DMs or RS products (Bjordal, 2018; Wullschleger et al., 2014), specific for the high latitudes (Druel
534 et al., 2017).

535 5.2 Sensitivity experiments

536 Adjusting DGVM parameters so that they correspond better with environmental drivers known to be functional in
537 the high-latitude PFTs has been suggested as a measure to improve the performance of DGVM (Wullschleger et
538 al., 2014). Our sensitivity experiments demonstrate that DM results can inform DGVM parameterisation based
539 upon suitability ranges of the environmental predictors recognized by DM in determining the distribution of a
540 PFT. Most notably, we recognize that the implementation of precipitation seasonality ($\text{bioclim}_{15} < 50$) as a
541 threshold for the establishment of NET, which has not yet been used in the DGVM, improves the distribution of
542 high-latitude PFTs simulated by the DGVM. This adds to the environmental thresholds for establishment of a PFT
543 previously used in DGVMs to restrict the predicted distribution of PFTs to realistic geographic regions (Miller and
544 Smith, 2012). Even though our sensitivity experiments focus on a limited number of additional thresholds across
545 three PFTs, this approach shows promising results and is worth exploring more extensively in future studies.

546 The importance of precipitation seasonality (i.e. bioclim_{15}) as a critical limiting factor for the establishment of
547 boreal NET indicates that the increased seasonality impedes growth of boreal NET. While some studies have
548 emphasized the importance of seasonal distribution of rainfall on vegetation in the semi-arid areas (Zhang et al.,
549 2018), the importance of this factor for high-altitude areas is less well studied (Oksanen, 1995; Sevanto et al.,
550 2006). Better representation of the processes related to the response of boreal NET to water availability, especially
551 spring-drought in DGVM, also warrants further investigation. From our results for plots 17 and 18, we notice that
552 adjusting the climatic thresholds for the establishment of boreal NET does not necessarily lead to other PFTs grow.
553 Boreal BDT and BDS can establish at both plots, but their growth rates are too slow to make them occupy a large
554 area at these plots. This implies that other environmental conditions, e.g., nitrogen availability, might play a more
555 important role in limiting the growth of BDT and BDS in the tested DGVM. The biases of the DGVM in simulating
556 BDT and BDS has been widely noticed in previous studies (Castillo et al., 2012), and remains a challenge requiring
557 more investigation in the future.

558 While going into further details of which additional PFTs should be included in DGVMs and how these and other
559 PFTs should be parameterised is beyond the scope of the present paper, we emphasize the potential of using DM
560 for improving the parameters of DGVMs. More specifically, we propose more intensive exploration of DM as a
561 tool for identification of potential environmental drivers for the high-latitude PFTs, which may enhance the
562 performance of DGVMs in high-latitude ecoregions. The specific focus of our study is the boreal region, both
563 because of the importance of these ecosystems in the climate system and because of the data availability of
564 vegetation-type DM and the field-based reference dataset (AR). However, we believe that the improved DGVM
565 parameters resulting from our sensitivity experiments may be applicable to other DGVMs such as TEM and LPJ-
566 GUESS (Euskirchen et al., 2009; Miller and Smith, 2012). Also, the results from this study are likely to be
567 transferable to other high-latitude areas in the circumboreal region.

568 6 Conclusions

569 This study demonstrates the potential of using distribution models (DM) for representing present-day vegetation
570 in evaluations of plant functional type (PFT) distributions simulated by dynamic global vegetation models
571 (DGVMs) and for improvement of specific PFT parameters within DGVMs. By identification of the main
572 differences among PFT profiles obtained by three methods (DGVM, RS and DM) in selected high-latitude plots

573 distributed across climatic gradients in Norway, we show that PFT profiles derived from DM and RS are in the
574 same range of reliability, judged by resemblance to a reference dataset (AR). Hence, we suggest that DM results
575 can be used as a complementary evaluation dataset to benchmark the present-day DGVMs. This approach is
576 recommended when high-quality RS products are not available in desired thematic resolution or when they are not
577 able to supply proxies of other properties (such as deriving parameter improvements or PFT-specific traits).
578 Comparing the twenty PFT profiles obtained by DGVM with those obtained by AR shows a large overestimation
579 by DGVM of boreal needleleaf evergreen trees (boreal NET) and bare ground at the expense of boreal broadleaf
580 deciduous trees and shrubs. This is attributed to missing processes and PFT parameterizations of high-latitude
581 PFTs in DGVM. We use DM results to identify a new PFT-specific environmental parameter – precipitation
582 seasonality – which, in a series of sensitivity experiments, improves the distribution of boreal NET predicted by
583 DGVM. This new PFT-specific threshold for establishment decreases the bias of boreal NET in DGVM across
584 four out of six plots and as a result, the distribution of other high-latitude PFTs is also better represented. We argue
585 that this new threshold should be transferable to other DGVMs simulating high-latitude PFTs, and that our DM-
586 based approach can be well applied to other ecosystems.
587 Further development of DGVM, such as refining parameters for existing boreal PFTs and increasing the thematic
588 resolution of PFTs for boreal areas, should be strongly encouraged to achieve a more realistic simulation of the
589 distribution of vegetation by DGVM, to increase the reliability of future predictions, and the reliability of predicted
590 vegetation feedbacks in the climate system.

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595 **8 Data availability.**

596 The model scripts for running the DGVM are available in the GitHub repository [https://github.com/huitang-
597 earth/Horvath_etal_BG2020](https://github.com/huitang-earth/Horvath_etal_BG2020), while the script used to carry out the analysis of this study is available in the GitHub
598 repository https://github.com/geco-nhm/DGVM_RS_DM_Norway. High-resolution DM-based and RS-based
599 PFT maps are available for download at the Dryad Digital Repository <https://doi.org/10.5061/dryad.dfn2z34xn>
600 (Fig. S9). DGVM outputs are provided in the Table S10, Table S13 and Fig. S11.

601 **9 Author contributions.**

602 All authors have contributed to conceptualizing the research idea. PH curated the data and was responsible for the
603 distribution modelling and for compiling and analysing the data from all methods. HT carried out the modelling
604 and sensitivity tests using the DGVM (CLM4.5-BGCDV). PH together with AB, RH and HT were responsible for
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607 **10 Competing interests.**

608 The authors declare that they have no conflict of interest.

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613 **12 References:**

614 Alexander, R., and Millington, A. C.: Vegetation mapping: From Patch to Planet, Vegetation Mapping, John Wiley
615 & Sons, LTD, Chichester, England, 321-331 pp., 2000.

616 Álvarez-Martínez, J. M., Jiménez-Alfaro, B., Barquín, J., Ondiviela, B., Recio, M., Silió-Calzada, A., and Juanes,
617 J. A.: Modelling the area of occupancy of habitat types with remote sensing, *Methods in Ecology and Evolution*,
618 9, 580-593, <https://doi.org/10.1111/2041-210X.12925>, 2018.

619 Assal, T. J., Anderson, P. J., and Sibold, J.: Mapping forest functional type in a forest-shrubland ecotone using
620 SPOT imagery and predictive habitat distribution modelling, *Remote Sensing Letters*, 6, 755-764,
621 <https://doi.org/10.1080/2150704x.2015.1072289>, 2015.

622 Bakkestuen, V., Erikstad, L., and Halvorsen, R.: Step-less models for regional environmental variation in Norway,
623 *J. Biogeogr.*, 35, 1906-1922, <https://doi.org/10.1111/j.1365-2699.2008.01941.x>, 2008.

624 Bjordal, J.: Potential Implications of Lichen Cover for the Surface Energy Balance: Implementing Lichen as a new
625 Plant Functional Type in the Community Land Model (CLM4.5), Master Thesis, Department of Geosciences,
626 University of Oslo, Oslo, 99 pp., 2018.

627 Bohn, U., Gollub, G., Hettwer, C., Neuhäuslova, Z., Raus, T., Schlüter, H., and Weber, H.: Map of the Natural
628 Vegetation of Europe. Scale 1 : 2 500 000., Federal Agency for Nature Conservation, Münster, 2000.

629 Bonan, G. B., Levis, S., Kergoat, L., and Oleson, K. W.: Landscapes as patches of plant functional types: An
630 integrating concept for climate and ecosystem models, *Global Biogeochemical Cycles*, 16, 5-1-5-23,
631 <https://doi.org/10.1029/2000gb001360>, 2002.

632 Bonan, G. B., Levis, S., Sitch, S., Vertenstein, M., and Oleson, K. W.: A dynamic global vegetation model for use
633 with climate models: concepts and description of simulated vegetation dynamics, *Global Change Biol.*, 9, 1543-
634 1566, <https://doi.org/10.1046/j.1365-2486.2003.00681.x>, 2003.

635 Bonan, G. B.: Forests, Climate, and Public Policy: A 500-Year Interdisciplinary Odyssey, *Annual Review of*
636 *Ecology, Evolution, and Systematics*, 47, 97-121, <https://doi.org/10.1146/annurev-ecolsys-121415-032359>, 2016.

637 Bryn, A., Dramstad, W., Fjellstad, W., and Hofmeister, F.: Rule-based GIS-modelling for management purposes:
638 A case study from the islands of Froan, Sør-Trøndelag, mid-western Norway, *Norsk Geografisk Tidsskrift*, 64,
639 175-184, <https://doi.org/10.1080/00291951.2010.528224>, 2010.

640 Bryn, A., Dourojeanni, P., Hemsing, L. Ø., and O'Donnell, S.: A high-resolution GIS null model of potential forest
641 expansion following land use changes in Norway, *Scand. J. For. Res.*, 28, 81-98,
642 <https://doi.org/10.1080/02827581.2012.689005>, 2013.

643 Bryn, A., Strand, G.-H., Angeloff, M., and Rekdal, Y.: Land cover in Norway based on an area frame survey of
644 vegetation types, *Norsk Geografisk Tidsskrift-Norwegian Journal of Geography*, 72, 1-15,
645 <https://doi.org/10.1080/00291951.2018.1468356>, 2018.

- 646 Chadburn, S. E., Burke, E. J., Essery, R. L. H., Boike, J., Langer, M., Heikenfeld, M., Cox, P. M., and
647 Friedlingstein, P.: Impact of model developments on present and future simulations of permafrost in a global land-
648 surface model, *The Cryosphere*, 9, 1505-1521, 10.5194/tc-9-1505-2015, 2015.
- 649 Coppel, R., Gloor, E., and Holden, J.: A process-based Sphagnum plant-functional-type model for implementation
650 in the TRIFFID Dynamic Global Vegetation Model, *Geosci. Model Dev. Discuss.*, 2019, 1-44, 10.5194/gmd-
651 2019-51, 2019.
- 652 Czekanowski, J.: Zur differentialdiagnose der Neandertalgruppe, Friedr. Vieweg & Sohn, 1909.
- 653 Dallmeyer, A., Claussen, M., and Brovkin, V.: Harmonising plant functional type distributions for evaluating Earth
654 System Models, *Climate of the Past*, 15, 335-366, <https://doi.org/10.5194/cp-15-335-2019>, 2019.
- 655 Davin, E. L., and de Noblet-Ducoudré, N.: Climatic Impact of Global-Scale Deforestation: Radiative versus
656 Nonradiative Processes, *J. Clim.*, 23, 97-112, <https://doi.org/10.1175/2009jcli3102.1>, 2010.
- 657 Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S.,
658 Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin,
659 V., Crist, E., Sechrest, W., Price, L., Baillie, J. E. M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R.,
660 Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pinteá, L., Brito, J. C., Llewellyn,
661 O. A., Miller, A. G., Patzelt, A., Ghazanfar, S. A., Timberlake, J., Kloser, H., Shennan-Farpon, Y., Kindt, R.,
662 Lilleso, J. B., van Breugel, P., Graudal, L., Vogé, M., Al-Shammari, K. F., and Saleem, M.: An Ecoregion-Based
663 Approach to Protecting Half the Terrestrial Realm, *Bioscience*, 67, 534-545, <https://doi.org/10.1093/biosci/bix014>,
664 2017.
- 665 Druel, A., Peylin, P., Krinner, G., Ciais, P., Viovy, N., Peregon, A., Bastrikov, V., Kosykh, N., and Mironycheva-
666 Tokareva, N.: Towards a more detailed representation of high-latitude vegetation in the global land surface model
667 ORCHIDEE (ORC-HL-VEGv1.0), *Geoscientific Model Development*, 10, 4693-4722,
668 <https://doi.org/10.5194/gmd-10-4693-2017>, 2017.
- 669 Druel, A., Ciais, P., Krinner, G., and Peylin, P.: Modeling the Vegetation Dynamics of Northern Shrubs and
670 Mosses in the ORCHIDEE Land Surface Model, *Journal of Advances in Modeling Earth Systems*, 11, 2020-2035,
671 10.1029/2018ms001531, 2019.
- 672 Duveiller, G., Hooker, J., and Cescatti, A.: The mark of vegetation change on Earth's surface energy balance,
673 *Nature Communications*, 9, 679, <https://doi.org/10.1038/s41467-017-02810-8>, 2018.
- 674 Dyrddal, A. V., Stordal, F., and Lussana, C.: Evaluation of summer precipitation from EURO-CORDEX fine-scale
675 RCM simulations over Norway, *International Journal of Climatology*, 38, 1661-1677,
676 <https://doi.org/10.1002/joc.5287>, 2018.
- 677 Eurostat: The Lucas Survey: European Statisticians Monitor Territory, Office for Official Publications of the
678 European Communities, Luxembourg, 2003.
- 679 Euskirchen, E. S., McGuire, A. D., Chapin III, F. S., Yi, S., and Thompson, C. C.: Changes in vegetation in
680 northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks, *Ecol. Appl.*,
681 19, 1022-1043, 10.1890/08-0806.1, 2009.
- 682 Ferrier, S., Watson, G., Pearce, J., and Drielsma, M.: Extended statistical approaches to modelling spatial pattern
683 in biodiversity in northeast New South Wales. I. Species-level modelling, *Conserv. Biol.*, 11, 2275-2307,
684 <https://doi.org/10.1023/a:1021302930424>, 2002.
- 685 Ferrier, S., and Guisan, A.: Spatial modelling of biodiversity at the community level, *J. Appl. Ecol.*, 43, 393-404,
686 <https://doi.org/10.1111/j.1365-2664.2006.01149.x>, 2006.
- 687 Fielding, A. H., and Bell, J. F.: A review of methods for the assessment of prediction errors in conservation
688 presence/absence models, *Environ. Conserv.*, 24, 38-49, 1997.

689 Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C., Meir, P., and Ian
690 Woodward, F.: Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological
691 scale limitations, *New Phytol.*, 187, 666-681, <https://doi.org/10.1111/j.1469-8137.2010.03340.x>, 2010.

692 Franklin, S. E., and Wulder, M. A.: Remote sensing methods in medium spatial resolution satellite data land cover
693 classification of large areas, *Progress in Physical Geography*, 26, 173-205,
694 <https://doi.org/10.1191/0309133302pp332ra>, 2002.

695 Førland, E.: Precipitation and topography [in Norwegian with English summary], *Klima*, 79, 23–24, 1979.

696 Gotangco Castillo, C. K., Levis, S., and Thornton, P.: Evaluation of the New CNDV Option of the Community
697 Land Model: Effects of Dynamic Vegetation and Interactive Nitrogen on CLM4 Means and Variability, *J. Clim.*,
698 25, 3702-3714, <https://doi.org/10.1175/jcli-d-11-00372.1>, 2012.

699 Halvorsen, R.: A gradient analytic perspective on distribution modelling, *Sommerfeltia*, 35, 1-165,
700 <https://doi.org/10.2478/v10208-011-0015-3>, 2012.

701 Hanssen-Bauer, I., Førland, E., Haddeland, I., Hisdal, H., Lawrence, D., Mayer, S., Nesje, A., Nilsen, J., Sandven,
702 S., and Sandø, A.: Climate in Norway 2100—A knowledge base for climate adaptation, The Norwegian Centre for
703 Climate Services, The Norwegian Centre for Climate Services, 2017.

704 Hartley, A. J., MacBean, N., Georgievski, G., and Bontemps, S.: Uncertainty in plant functional type distributions
705 and its impact on land surface models, *Remote Sens. Environ.*, 203, 71-89,
706 <https://doi.org/10.1016/j.rse.2017.07.037>, 2017.

707 Hemsing, L. Ø., and Bryn, A.: Three methods for modelling potential natural vegetation (PNV) compared: A
708 methodological case study from south-central Norway, *Norsk Geografisk Tidsskrift - Norwegian Journal of*
709 *Geography*, 66, 11-29, <https://doi.org/10.1080/00291951.2011.644321>, 2012.

710 Henderson, E. B., Ohmann, J. L., Gregory, M. J., Roberts, H. M., and Zald, H.: Species distribution modelling for
711 plant communities: stacked single species or multivariate modelling approaches?, *Applied Vegetation Science*, 17,
712 516-527, <https://doi.org/10.1111/avsc.12085>, 2014.

713 Hengl, T., Walsh, M. G., Sanderman, J., Wheeler, I., Harrison, S. P., and Prentice, I. C.: Global mapping of
714 potential natural vegetation: an assessment of machine learning algorithms for estimating land potential, *PeerJ*, 6,
715 e5457, <https://doi.org/10.7717/peerj.5457>, 2018.

716 Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T. R.,
717 Cramer, W., Kuhn, I., and Sykes, M. T.: Projecting the future distribution of European potential natural vegetation
718 zones with a generalized, tree species-based dynamic vegetation model, *Global Ecol. Biogeogr.*, 21, 50-63,
719 <https://doi.org/10.1111/j.1466-8238.2010.00613.x>, 2012.

720 Horvath, P., Halvorsen, R., Stordal, F., Tallaksen, L. M., Tang, H., and Bryn, A.: Distribution modelling of
721 vegetation types based on area frame survey data, *Applied Vegetation Science*, 22, 547-560,
722 <https://doi.org/10.1111/avsc.12451>, 2019.

723 Johansen, B. E.: Satellittbasert vegetasjonskartlegging for Norge, Direktoratet for Naturforvaltning, Norsk
724 Romsenter, 2009.

725 Keith, D. A., Ferrer, J. R., Nicholson, E., Bishop, M. J., Polidoro, B. A., Llodra, E. R., Tozer, M. G., Nel, J. L.,
726 Nally, R. M., Gregr, E. J., Watermeyer, K. E., Essl, F., Faber-Langendoen, D., Franklin, J., Lehmann, C. E. R.,
727 Etter, A., Roux, D. J., Stark, J. S., Rowland, J. A., Brummitt, N. A., Fernandez-Arcaya, U. C., Suthers, I. M.,
728 Wiser, S. K., Donohue, I., Jackson, L. J., Pennington, R. T., Pettorelli, N., Andrade, A., Kontula, T., Lindgaard,
729 A., Tahvanainen, T., Terauds, A., Venter, O., Watson, J. E. M., Chadwick, M. A., Murray, N. J., Moat, J., Pliscoff,
730 P., Zager, I., and Kingsford, R. T.: The IUCN Global Ecosystem Typology v1.01: Descriptive profiles for Biomes
731 and Ecosystem Functional Groups, IUCN, CEM, New York, 172, 2020.

732 Lantz, T. C., Gergel, S. E., and Kokelj, S. V.: Spatial Heterogeneity in the Shrub Tundra Ecotone in the Mackenzie
733 Delta Region, Northwest Territories: Implications for Arctic Environmental Change, *Ecosystems*, 13, 194-204,
734 [10.1007/s10021-009-9310-0](https://doi.org/10.1007/s10021-009-9310-0), 2010.

- 735 Lawrence, D. M., Oleson, K. W., Flanner, M. G., Thornton, P. E., Swenson, S. C., Lawrence, P. J., Zeng, X.,
736 Yang, Z. L., Levis, S., and Sakaguchi, K.: Parameterization improvements and functional and structural advances
737 in version 4 of the Community Land Model, *Journal of Advances in Modeling Earth Systems*, 3,
738 <https://doi.org/10.1029/2011MS00045>, 2011.
- 739 Lawrence, P. J., and Chase, T. N.: Representing a new MODIS consistent land surface in the Community Land
740 Model (CLM 3.0), *Journal of Geophysical Research*, 112, n/a-n/a, <https://doi.org/10.1029/2006jg000168>, 2007.
- 741 Levis, S., Bonan, B., Vertenstein, M., and Oleson, K.: The community land model's dynamic global vegetation
742 model (CLM-DGVM): technical description and user's guide, National Center for Atmospheric Research, Boulder,
743 Colorado, 2004.
- 744 Li, W., Ciais, P., MacBean, N., Peng, S., Defourny, P., and Bontemps, S.: Major forest changes and land cover
745 transitions based on plant functional types derived from the ESA CCI Land Cover product, *International Journal*
746 *of Applied Earth Observation and Geoinformation*, 47, 30-39, <https://doi.org/10.1016/j.jag.2015.12.006>, 2016.
- 747 Li, W., MacBean, N., Ciais, P., Defourny, P., Lamarche, C., Bontemps, S., Houghton, R. A., and Peng, S.: Gross
748 and net land cover changes in the main plant functional types derived from the annual ESA CCI land cover maps
749 (1992–2015), *Earth Syst. Sci. Data*, 10, 219-234, <https://doi.org/10.5194/essd-10-219-2018>, 2018.
- 750 Lussana, C., Saloranta, T., Skaugen, T., Magnusson, J., Tveito, O. E., and Andersen, J.: seNorge2 daily
751 precipitation, an observational gridded dataset over Norway from 1957 to the present day, *Earth System Science*
752 *Data*, 10, 235-249, <https://doi.org/10.5194/essd-10-235-2018>, 2018a.
- 753 Lussana, C., Tveito, O., and Uboldi, F.: Three-dimensional spatial interpolation of 2 m temperature over Norway,
754 *Quarterly Journal of the Royal Meteorological Society*, 144, 344-364, <https://doi.org/10.1002/qj.3208>, 2018b.
- 755 Majasalmi, T., Eisner, S., Astrup, R., Fridman, J., and Bright, R. M.: An enhanced forest classification scheme for
756 modeling vegetation–climate interactions based on national forest inventory data, *Biogeosciences*, 15, 399-412,
757 10.5194/bg-15-399-2018, 2018.
- 758 Miller, P. A., and Smith, B.: Modelling Tundra Vegetation Response to Recent Arctic Warming, *Ambio*, 41, 281-
759 291, <https://doi.org/10.1007/s13280-012-0306-1>, 2012.
- 760 Moen, A.: *Vegetation, Norwegian Mapping Authority, Hønefoss, 200 s. ill. 234 cm pp., 1999.*
- 761 Mùcher, C. A., Hennekens, S. M., Bunce, R. G. H., Schaminée, J. H. J., and Schaepman, M. E.: Modelling the
762 spatial distribution of Natura 2000 habitats across Europe, *Landscape Urban Plann.*, 92, 148-159,
763 <https://doi.org/10.1016/j.landurbplan.2009.04.003>, 2009.
- 764 Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria,
765 M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers,
766 S., Rozema, J., Rayback, S. A., Schmidt, N. M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C. B., Venn,
767 S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H. E., and Hik,
768 D. S.: Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities, *Environmental Research*
769 *Letters*, 6, 045509, <https://doi.org/10.1088/1748-9326/6/4/045509>, 2011.
- 770 Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-
771 Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A.,
772 Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., Forbes, B. C., Goetz, S. J., Hollister,
773 R. D., de Jong, R., Loranty, M. M., Macias-Fauria, M., Maseyk, K., Normand, S., Olofsson, J., Parker, T. C.,
774 Parmentier, F.-J. W., Post, E., Schaepman-Strub, G., Stordal, F., Sullivan, P. F., Thomas, H. J. D., Tømmervik,
775 H., Treharne, R., Tweedie, C. E., Walker, D. A., Wilmking, M., and Wipf, S.: Complexity revealed in the greening
776 of the Arctic, *Nature Climate Change*, 10, 106-117, <https://doi.org/10.1038/s41558-019-0688-1>, 2020.
- 777 O'Donnell, M. S., and Ignizio, D. A.: Bioclimatic predictors for supporting ecological applications in the
778 conterminous United States, 2012.
- 779 Oksanen, L.: Isolated occurrences of spruce, *Picea abies*, in northernmost Fennoscandia in relation to the enigma
780 of continental mountain birch forests, *Acta Bot. Fenn.*, 81-92, 1995.

- 781 Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis, S., Li, F., Riley,
782 W. J., Subin, Z. M., Swenson, S. C., and Thornton, P. E.: Technical Description of version 4.5 of the Community
783 Land Model (CLM), NCAR Earth System Laboratory Climate and Global Dynamics Division, BOULDER,
784 COLORADO, USA, 2013.
- 785 Pebesma, E. J., and Bivand, R. S.: Classes and methods for spatial data in {R}, *R News*, 5, 9-13, 2005.
- 786 Porada, P., Ekici, A., and Beer, C.: Effects of bryophyte and lichen cover on permafrost soil temperature at large
787 scale, *The Cryosphere*, 10, 2291-2315, [10.5194/tc-10-2291-2016](https://doi.org/10.5194/tc-10-2291-2016), 2016.
- 788 Poulter, B., Ciais, P., Hodson, E., Lischke, H., Maignan, F., Plummer, S., and Zimmermann, N. E.: Plant functional
789 type mapping for earth system models, *Geoscientific Model Development*, 4, 993-1010,
790 <https://doi.org/10.5194/gmd-4-993-2011>, 2011.
- 791 Poulter, B., MacBean, N., Hartley, A., Khlystova, I., Arino, O., Betts, R., Bontemps, S., Boettcher, M.,
792 Brockmann, C., Defourny, P., Hagemann, S., Herold, M., Kirches, G., Lamarche, C., Lederer, D., Ottlé, C., Peters,
793 M., and Peylin, P.: Plant functional type classification for earth system models: results from the European Space
794 Agency's Land Cover Climate Change Initiative, *Geosci. Model Dev.*, 8, 2315-2328, <https://doi.org/10.5194/gmd-8-2315-2015>, 2015.
- 796 Scheiter, S., Langan, L., and Higgins, S. I.: Next-generation dynamic global vegetation models: learning from
797 community ecology, *New Phytol.*, 198, 957-969, <https://doi.org/10.1111/nph.12210>, 2013.
- 798 Seo, H., and Kim, Y.: Interactive impacts of fire and vegetation dynamics on global carbon and water budget using
799 Community Land Model version 4.5, *Geoscientific Model Development*, 12, 457-472,
800 <https://doi.org/10.5194/gmd-12-457-2019>, 2019.
- 801 Sevanto, S., Suni, T., Pumpanen, J., Grönholm, T., Kolari, P., Nikinmaa, E., Hari, P., and Vesala, T.: Wintertime
802 photosynthesis and water uptake in a boreal forest, *Tree Physiology*, 26, 749-757,
803 <https://doi.org/10.1093/treephys/26.6.749>, 2006.
- 804 Shi, Y., Yu, M., Erfanian, A., and Wang, G.: Modeling the Dynamic Vegetation–Climate System over China Using
805 a Coupled Regional Model, *J. Clim.*, 31, 6027-6049, [10.1175/jcli-d-17-0191.1](https://doi.org/10.1175/jcli-d-17-0191.1), 2018.
- 806 Simensen, T., Horvath, P., Erikstad, L., Bryn, A., Vollering, J., and Halvorsen, R.: Composite landscape predictors
807 improve distribution models of ecosystem types, *Divers. Distrib.*, <https://doi.org/10.1111/ddi.13060>, 2020.
- 808 Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R., Ciais, P., Cox, P.,
809 Friedlingstein, P., Jones, C. D., Prentice, I. C., and Woodward, F. I.: Evaluation of the terrestrial carbon cycle,
810 future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models
811 (DGVMs), *Global Change Biol.*, 14, 2015-2039, <https://doi.org/10.1111/j.1365-2486.2008.01626.x>, 2008.
- 812 Snell, R. S., Huth, A., Nabel, J. E. M. S., Bocedi, G., Travis, J. M. J., Gravel, D., Bugmann, H., Gutiérrez, A. G.,
813 Hickler, T., Higgins, S. I., Reineking, B., Scherstjanoi, M., Zurbriggen, N., and Lischke, H.: Using dynamic
814 vegetation models to simulate plant range shifts, *Ecography*, 37, 1184-1197, <https://doi.org/10.1111/ecog.00580>,
815 2014.
- 816 Song, X., Zeng, X., and Zhu, J.: Evaluating the tree population density and its impacts in CLM-DGVM, *Advances*
817 *in Atmospheric Sciences*, 30, 116-124, <https://doi.org/10.1007/s00376-012-1271-0>, 2013.
- 818 Strand, G.-H.: The Norwegian area frame survey of land cover and outfield land resources, *Norsk Geografisk*
819 *Tidsskrift*, 67, 24-35, <https://doi.org/10.1080/00291951.2012.760001>, 2013.
- 820 Ullerud, H. A., Bryn, A., and Klanderud, K.: Distribution modelling of vegetation types in the boreal–alpine
821 ecotone, *Applied Vegetation Science*, 19, 528-540, <https://doi.org/10.1111/avsc.12236>, 2016.
- 822 Ullerud, H. A., Bryn, A., and Skånes, H.: Bridging theory and implementation – Testing an abstract classification
823 system for practical mapping by field survey and 3D aerial photographic interpretation, *Norsk Geografisk*
824 *Tidsskrift*, 73, 301-317, <https://doi.org/10.1080/00291951.2020.1717595>, 2020.

- 825 Vowles, T., Gunnarsson, B., Molau, U., Hickler, T., Klemedtsson, L., and Björk, R. G.: Expansion of deciduous
826 tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range, *J. Ecol.*, 105, 1547-
827 1561, <https://doi.org/10.1111/1365-2745.12753>, 2017.
- 828 Wielgolaski, F. E.: History and Environment of the Nordic Mountain Birch, in: *Plant Ecology, Herbivory, and*
829 *Human Impact in Nordic Mountain Birch Forests*, edited by: Caldwell, M. M., Heldmaier, G., Jackson, R. B.,
830 Lange, O. L., Mooney, H. A., Schulze, E. D., Sommer, U., Wielgolaski, F. E., Karlsson, P. S., Neuvonen, S., and
831 Thannheiser, D., *Ecological Studies*, Springer Berlin Heidelberg, Berlin, Heidelberg, 3-18, 2005.
- 832 Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., Kattge, J., Norby,
833 R. J., van Bodegom, P. M., and Xu, X.: Plant functional types in Earth system models: past experiences and future
834 directions for application of dynamic vegetation models in high-latitude ecosystems, *Ann. Bot.*, 114, 1-16,
835 <https://doi.org/10.1093/aob/mcu077>, 2014.
- 836 Xie, Y., Sha, Z., and Yu, M.: Remote sensing imagery in vegetation mapping: a review, *Journal of Plant Ecology*,
837 1, 9-23, <https://doi.org/10.1093/jpe/rtm005>, 2008.
- 838 Zeng, X., Zeng, X., and Barlage, M.: Growing temperate shrubs over arid and semiarid regions in the Community
839 Land Model–Dynamic Global Vegetation Model, *Global Biogeochemical Cycles*, 22, n/a-n/a,
840 <https://doi.org/10.1029/2007gb003014>, 2008.
- 841 Zhang, W., Brandt, M., Tong, X., Tian, Q., and Fensholt, R.: Impacts of the seasonal distribution of rainfall on
842 vegetation productivity across the Sahel, *Biogeosciences*, 15, 319-330, <https://doi.org/10.5194/bg-15-319-2018>,
843 2018.
- 844 Zhu, J., Zeng, X., Zhang, M., Dai, Y., Ji, D., Li, F., Zhang, Q., Zhang, H., and Song, X.: Evaluation of the New
845 Dynamic Global Vegetation Model in CAS-ESM, *Advances in Atmospheric Sciences*, 35, 659-670,
846 <https://doi.org/10.1007/s00376-017-7154-7>, 2018.
- 847 Zuur, A. F., Ieno, E. N., and Smith, G. M.: *Analysing ecological data*, in, Springer, New York, 163-178, 2007.
848