

Modelling Tundra Vegetation Response to Recent Arctic Warming

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Abstract The Arctic land area has warmed by >1 °C in the last 30 years and there is evidence that this has led to increased productivity and stature of tundra vegetation and reduced albedo, effecting a positive (amplifying) feedback to climate warming. We applied an individual-based dynamic vegetation model over the Arctic forced by observed climate and atmospheric CO₂ for 1980-2006. Averaged over the study area, the model simulated increases in primary production and leaf area index, and an increasing representation of shrubs and trees in vegetation. The main underlying mechanism was a warming-driven increase in growing season length, enhancing the production of shrubs and trees to the detriment of shaded ground-level vegetation. The simulated vegetation changes were estimated to correspond to a 1.75 % decline in snow-season albedo. Implications for modelling future climate impacts on Arctic ecosystems and for the incorporation of biogeophysical feedback mechanisms in Arctic system models are discussed.

Keywords Arctic tundra vegetation · Climate change · Shrub expansion · Ecosystem modelling · LPJ-GUESS · Biogeophysical feedbacks

INTRODUCTION

The climates of the polar regions rank among the harshest on Earth due to the conditions imposed on biological activity by extremely low seasonal temperatures, a low annual radiation budget and other factors, such as low nutrient mineralisation rates, arising from these primary stresses. Amelioration of low temperatures by global warming-believed to be proceeding more rapidly in the Arctic compared to the Northern Hemisphere generally (McBean et al. 2005)-may be expected to have a substantial influence on the activity of organisms and the structure and functioning of ecosystems of the Arctic (Callaghan et al. 2005). Changes in Arctic plant communities may already be taking place in response to warming over recent decades. Important lines of evidence include positive trends in surface greenness and photosynthetic activity inferred from satellite data (Tucker et al. 2001; Bunn and Goetz 2006; Bhatt et al. 2010; Beck and Goetz 2011), advancement of elevational and latitudinal treelines (Sonesson and Hoogesteger 1983; Kullman 2002; Harsch et al. 2009; Van Bogaert et al. 2010, 2011), and an increased cover, abundance and stature of shrubs in tundra areas (Kullman 2002; Jia et al. 2003; Tømmervik et al. 2004; Tape et al. 2006; Hedenås et al. 2011; Rundqvist et al. 2011). Despite numerous local exceptions, the weight of evidence from observational studies suggests that, in general, Arctic vegetation is responding to rising temperatures through increases in productivity, density, cover and stature of vegetation and, in many areas, an increase in woody biomass and the representation of trees and shrubs (Post et al. 2009; Callaghan et al. 2011; Elmendorf et al. 2012). These findings are qualitatively consistent with expectations based on the results of tundra warming experiments (Chapin et al. 1995; Michelsen et al. 1996; Arft et al. 1999; Graglia et al. 2001; Walker et al. 2006; Olsrud et al. 2010), and simulations using vegetation models (Kaplan et al. 2003; Smith et al. 2008a; Wolf et al. 2008a; Wramneby et al. 2010).

Arctic vegetation change is not just an issue of ecological interest or concern. Ecosystems are part of the

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climate system, changes in land cover, vegetation structure and phenology feeding back to the atmosphere through changes in near-surface energy, water and momentum fluxes (Claussen et al. 2001). At high latitudes, feedbacks resulting from changes in albedo (reflectance of incoming solar radiation) associated with shrub expansion and treeline advance have received particular attention. A number of climate model-based studies have concluded that the decline in albedo resulting from the masking of snow by protruding trees and tall shrubs could amplify warming in affected areas to a degree comparable seasonally with the direct anthropogenic forcing of climate (Betts 2000; Claussen et al. 2001; Göttel et al. 2008; Wramneby et al. 2010; Matthes et al. 2012 Bonfils et al. 2012). Additional feedback mechanisms involving the effects of ecosystem changes on evapotranspiration and carbon balance are in general predicted to further amplify warming (Swann et al. 2010; Koven et al. 2011, Bonfils et al. 2012). Chapin et al. (2005) have estimated that albedo changes resulting from shrub expansion in arctic Alaska increased atmospheric heating locally by some 3 W m⁻² locally over the 1980s and 1990s. Arctic vegetation feedbacks may well be a contributing factor to the phenomenon of Arctic amplification of climate change (McBean et al. 2005).

Projecting the impacts of future climate change on vegetation patterns across the Arctic can be accomplished using models. Although models incorporating some of the specific features of Arctic plant species and biomes are beginning to emerge (Kaplan et al. 2003; Wolf et al. 2008a), most studies to date have employed global models based on highly generalised plant functional types (PFTs) such as 'boreal needle-leaved tree' and simplified descriptions of the climate-dependent mechanisms governing their distribution and dynamics. Such oversimplification may account for a suggested tendency for the models to overestimate rates of forest migration, or to underestimate changes in woody plant density and cover in response to warming, when compared with historical studies (Callaghan et al. 2011). Improved, Arctic-enabled models are needed to provide adequate descriptions of Arctic vegetation change, and for coupling to regional and global Earth system models, accounting for the feedbacks that could significantly amplify climate change at higher latitudes (Roberts et al. 2010).

Synthesising findings from studies that have tracked changes in Arctic tundra vegetation over recent decades, Callaghan et al. (2011) challenged modellers to use the findings to validate—and improve—the models. Here, we take on this challenge, applying a customised, Arctic version of the LPJ-GUESS dynamic vegetation model (Smith et al. 2001) across the Arctic, forced by climate data for the past three decades, during which the region has experienced a net warming of >1 °C. We compare the vegetation

dynamics simulated by the model to impacts reported from observational studies, and focus particular attention on vegetation-mediated changes in albedo and their implications for the forcing of Arctic climate.

MATERIALS AND METHODS

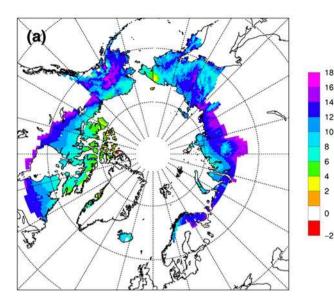
Model Domain and Study Period

The spatial domain for our study corresponds approximately to the extant distribution of the Arctic tundra biome. It was defined by the Global Carbon Project's Regional Carbon Cycle Assessment and Processes (RECCAP) activity to be potentially resolvable by atmospheric inversion models, and used in the RECCAP study of regional carbon balance from 1990 to 2006 (McGuire et al. 2012), which includes simulation results from LPJ-GUESS. The limits of the domain extend south of the tundra-taiga boundary in some regions, e.g. in Alaska. Figure 1a shows average July temperatures for the study domain. These vary from -2 °C in the Canadian Archipelago to near 18 °C in some southerly areas.

Our study focuses on the time period 1980–2006. This period is the same as that covered by recent studies documenting productivity and biomass changes in Arctic environments as derived from satellite measurements, for example, Bhatt et al. (2010), Beck and Goetz (2011), Goetz et al. (2011) and Piao et al. (2011). It also encompasses the 1990–2006 period studied by McGuire et al. (2012) for the purposes of constraining a carbon balance for the Arctic.

Dynamic Vegetation Model

Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS; Smith et al. 2001) is a process-based model of vegetation dynamics and biogeochemistry optimised for regional applications. The simulated vegetation dynamics are the emergent outcome of competition for light and soil water between co-occurring plant individuals, each belonging to one of a defined set of PFTs distinguished by allometry, phenology, shade tolerance and bioclimatic limits; see below and Tables S1-S4 in Appendix (Electronic Supplementary Material). For this study, we employed a customised, Arctic implementation of LPJ-GUESS, adopting an identical configuration to that described in McGuire et al. (2012). Compared with the standard version of the model (Smith et al. 2001; Hickler et al. 2012), the Arctic version includes differentiated representations of processes operating in upland and peatland ecosystems of the tundra and taiga biomes, as well as PFTs characteristic of Arctic ecosystems: evergreen and



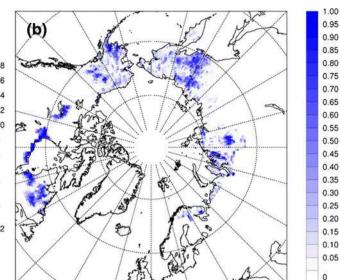


Fig. 1 a Average July temperature (°C) over the period 1978–2006 from the CRU TS 3.0 dataset of Mitchell and Jones (2005) for the tundra domain considered in this study (and McGuire et al. 2012);

deciduous shrubs, forbs, graminoids and bryophytes. The model includes an improved description of soil freezing processes (affecting water available to plants), based on Wania et al. (2009).

LPJ-GUESS has been used and evaluated in numerous studies; see for example, Smith et al. (2001, 2008b), Hickler et al. (2012) and references therein. For the tundra domain used here, McGuire et al. (2012) show that LPJ-GUESS agreed with observations, inverse modelling and three other process-based ecosystem models in predicting that the Arctic land area (same domain as this study) was a stronger carbon sink in 2000–2006 than in 1990–1999, but a greater source to the atmosphere of CH_4 . In addition, seasonal cycles of net primary production (NPP), heterotrophic respiration and net ecosystem productivity (NEP) simulated by the model over 1990–2006 were consistent with those inferred from inverse modelling.

Plant Functional Types

The 15 PFTs simulated by LPJ-GUESS in this study are listed in Table S1. More details of the traits distinguishing PFTs are given in Tables S2–S4. The five tree PFTs include both shade-tolerant (c.f. *Picea* spp.) and shade-intolerant (c.f. *Pinus* spp.) boreal evergreen conifers, the deciduous larch (*Larix* spp.), as well as broad-leaved deciduous trees (c.f. *Betula* spp.). We also adopted the Arctic-specific PFT definitions of Wolf et al. (2008a), encompassing deciduous and evergreen shrubs and four open-ground PFTs. The latter have no explicit height, but differ in their bioclimatic limits and association with snow (Table S3).

Simulation Protocol

pers. comm., Matthews and Fung 1987)

The model was run with 20 replicate patches in each grid cell, with simulations covering the time period from 1901 until 2006. Climate forcing at a resolution of $0.5^{\circ} \times 0.5^{\circ}$ consisted of monthly temperature, precipitation and cloudiness fields from the CRU TS 3.0 dataset of Mitchell and Jones (2005), and observed CO₂ concentrations. This historical phase of the simulations was preceded by a longer, "spin-up" phase in which the first 30 years of the climate data set were detrended and cycled repeatedly for 500 years in order to generate a vegetation and soil carbon state in equilibrium with the early twentieth-century climate. The CO₂ forcing was held fixed at the 1901 value of 296 ppmv for this spin-up period.

b peatland fraction in each 0.5° grid cell in the domain (D. Hayes,

For the study of McGuire et al. (2012), LPJ-GUESS was run twice for each grid cell, i.e. once with the standard LPJ-GUESS upland hydrology, and once with the peatland hydrology if the grid cell contained wetland. We do not consider the results of the wetland runs in this study, but we do use the fraction of wetland in each grid cell in the computation of grid cell average albedo (see below). The fraction of wetland in each grid cell (D. Hayes, pers. comm.; Matthews and Fung 1987) is assumed fixed throughout the study period and is shown in Fig. 1b. Areas with substantial wetland fractions include Alaska, western and eastern Siberia, and northern Canada.

Albedo Calculation

We calculated albedo for the winter (snow) and summer (snow-free) seasons as a weighed average of assumed

albedo constants for different vegetation classes, following the approach used by Wolf et al. (2008b) and Houldcroft et al. (2009). Details of the computations are described in Appendix S1 (Electronic Supplementary Material), while the albedo constants are given in Table S1.

RESULTS

Arctic Tundra Vegetation Change, 1980-2006

Figure 2 shows the dominant vegetation patterns as simulated by LPJ-GUESS for the 1980–2006 period. For comparison, remotely sensed vegetation patterns inferred from the MODIS sensor (UMD classification scheme; most popular class 2001–2006; DeFries et al. 1999; ORNL-DAAC 2011) are also shown. The overall patterns of vegetation across the study domain simulated by the model may also be discerned in the MODIS-based map, although the classes and classification schemes used to produce the two maps are different; in general the model's forest biome coincides with areas classified as forest or savannah in the MODIS dataset. The distribution of the modelled tundra distribution also compares favourably with the circumpolar Arctic vegetation map of Walker et al. (2005) (not shown).

Along a poleward axis through Canada, LPJ-GUESS simulates forest dominated by the evergreen, needle-leaved *Picea* and *Pinus* PFTs and by the deciduous broad-leaved PFT, which gives way to tall, shrub-dominated ecosystems and eventually tundra vegetation. The MODIS map, by comparison, shows a transition from forest and savannah to shrubland and, north of 76°N, grassland and barren ground. Note, however, that the modelled shrub category refers to tall shrubs up to 2 m in height, while the modelled tundra category includes both low shrubs up to 0.5 m in height and open-ground PFTs.

The simulated forest distribution is probably too extensive in the south-western tip of Alaska, where MO-DIS data classifies the area as shrubland and grassland. In western Siberia, the modelled forest gives way to shrub and then to tundra, with a similar transition from savannah to shrubland in the MODIS data. In central and eastern Siberia the dominant forest vegetation according to the model is the deciduous needle-leaved PFT, although the treeline is placed too far north in central Siberia, an artefact possibly attributable to a positive bias in summer temperatures in this region in the forcing climate data, as shown in Fig. 1a.

The interannual variability of domain-averaged leaf area index (LAI), gross primary production (GPP), and NPP are shown in Fig. 3, as well as the mean annual temperature and precipitation for the region and a time-series (1982– 2006) of observed annual maximum normalised difference vegetation index (MaxNDVI) for the tundra of the northern hemisphere, digitised from Fig. 7a in Bhatt et al. (2010). MaxNDVI is considered to be a useful proxy for tundra biomass (Bhatt et al. 2010). Consistent with the observed increase in MaxNDVI (Bhatt et al. 2010), LPJ-GUESS predicts an increasing LAI trend for the period, ranging from approximately 0.6 m² m⁻² in 1980 to approximately 0.8 m² m⁻² in 2006. GPP and NPP likewise increase over this period, both by approximately 30 %. The simulated grid-averaged NPP values are higher than the average value of 89 gC m⁻² year⁻¹ given by Huston and Wolverton (2009) for the tundra biome, but are augmented by values for the more productive boreal forest included in parts of our study domain.

A negative anomaly in LAI, GPP and NPP in 1991 may be traced to the cooling following the Mount Pinatubo volcano eruption, as discussed for the boreal region generally by Lucht et al. (2002). A similar anomaly is apparent in MaxNDVI (Fig. 3b).

The change in LAI for the forest and shrub biome classes over the study period is shown in Fig. 4. LAI increases almost uniformly in areas simulated to be dominated by trees (see Fig. 2). More modest and variable changes were simulated in areas simulated as dominated by shrubs. Increases in shrub LAI were simulated near the treeline in Canada, in northern Alaska, and in northwestern Eurasia. Decreases in shrub LAI also occur, particularly in the deciduous shrub-dominated ecosystems near (63°N, 110°W) in Canada, where the model predicts a larger presence of deciduous trees in 2006.

Albedo Change, 1980-2006

Winter albedo changes computed on the basis of our simulation results are shown in Fig. 5. Though area-averaged values (Table 1) indicate an albedo decline of 1.75 % in winter (Fig. 5) and a more modest 0.2 % decline in summer (map not shown), there is a large spatial variability in the winter albedo change. Most regions dominated by forest and shrubs (Fig. 2) show reductions in albedo, often up to 10 % or more, but there are also regions where winter albedo actually increases.

To highlight the mechanisms behind these changes, we focus on two grid cells in Canada, which exhibit contrasting albedo changes in the simulation. The uppermost time-series in Fig. 5 shows the vegetation composition at $(135^{\circ}W, 63^{\circ}N)$ to the east of the border with Alaska. This location has a mean annual temperature of $-5.1 \,^{\circ}C$, and July temperatures averaging 13 °C (Fig. 1a). There is a clear decline in albedo as the projective cover of tall shrubs, in particular the deciduous HSS PFT, increases from 1980 to 2006, while the fractions of both tundra and barren ground decrease. Over the study period, the

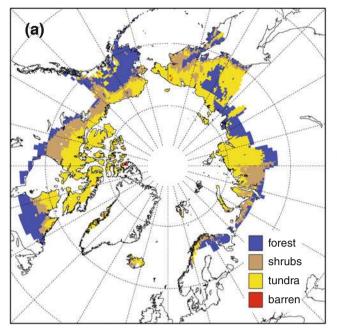
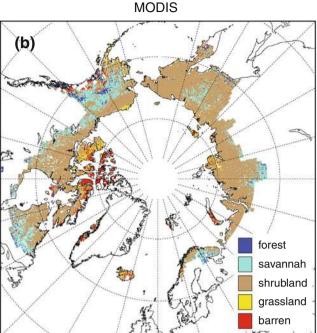
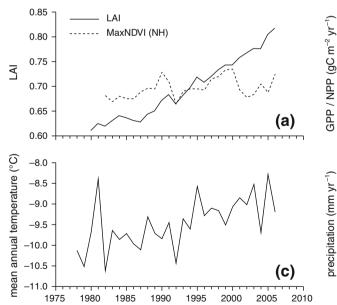


Fig. 2 a Simulated and b observed (MODIS) vegetation in the study area for 2001-2006. The class shown in a corresponds to the biome associated with the PFT simulated to have the greatest LAI in each grid cell (see Table S1, Online Supplementary Material). The modelled shrub category refers to tall shrubs, up to 2 m in height, while the modelled tundra category includes both low shrubs up to 0.5 m in height, and open-ground PFTs; see Table S1. MODIS classes



(b) are aggregated from the UMD classification scheme (DeFries et al. 1999; ORNL-DAAC 2011) as follows (UMD classes shown in parentheses): forest = (evergreen needleleaf forest + evergreen broadleaf forest + deciduous needleleaf forest + deciduous broadleaf forest + mixed forest); savannah = (woody savannas + savannas); shrubland = (closed)shrublands + open shrublands); grassland = (grasslands); barren = (barren or sparsely vegetated)



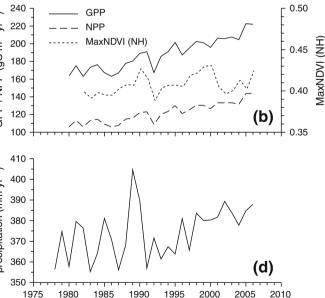


Fig. 3 Indicators of vegetation productivity, leaf area and biomass over the tundra domain considered in this study from 1980 to 2006: a modelled, area-averaged, total LAI (m² m⁻²) and observed annual maximum NDVI for the tundra of the northern hemisphere

(MaxNDVI (NH)) digitised from Fig. 7a in Bhatt et al. (2010); **b** MaxNDVI (NH) and modelled gross (GPP) (gC m⁻² year⁻¹) and net primary production (NPP) (gC m⁻² year⁻¹); c mean annual temperature (°C); **d** annual precipitation (mm)

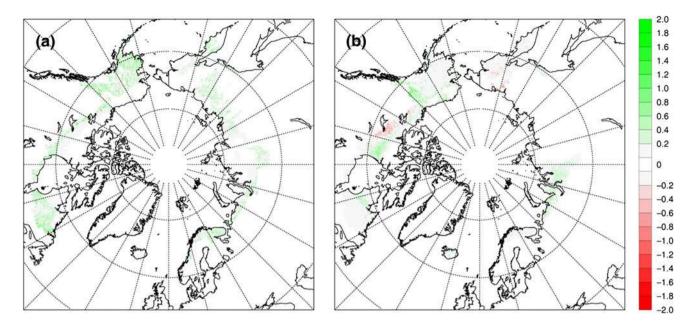


Fig. 4 Change in LAI (mean for 2003–2006 minus mean for 1980–1983), for **a** areas classified as forest in the simulations and **b** areas classified as shrubland in the simulations

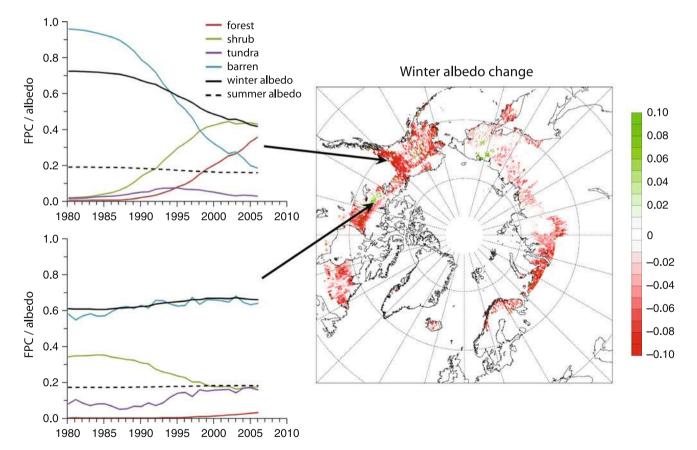


Fig. 5 Winter albedo change 1983–2006. Time-series at left show two representative examples of how simulated change in vegetation composition may alter winter and summer albedo. In the *lowermost* time-series (109.5°W, 64° N), a slight increase in albedo results as the

fractional cover of shrubs declines, with a simultaneous increase in the fraction of tundra vegetation. In the *uppermost* time-series (135°W, 63°N) albedo declines as the fractional cover of shrubs increases in response to rising summer and winter temperatures

Table 1 Winter and summer, total shortwave (0.3–5.0 µm), white-sky albedo values for the tundra domain computed from simulation results

	Winter	Winter	Winter change	Summer	Summer	Summer change
	1980–1983	2003–2006	1980–2006	1980–1983	2003–2006	1980–2006
Albedo	0.6764	0.6589	-0.0175	0.1693	0.1671	-0.0022

establishment, growth and survival of tall deciduous shrubs is promoted as a result of increasing summer temperatures, longer growing seasons and milder winters. Since the winter albedo associated with the HSS PFT is lower than the snow-covered barren and tundra (Table S1), this results in a decline in winter albedo for this grid cell.

The lowermost time-series in Fig. 5, corresponding to (109.5°W, 64°N) in central Canada (mean annual temperature -9.2 °C, mean July temperature 12.3 °C), illustrates that relatively small changes in vegetation structure in the simulation may lead to an appreciable albedo change (Fig. 1a). Here, winter albedo increases slightly as the shrub FPC declines from a maximum cover in the mid-1980s bringing with it a simultaneous increase in the fraction of barren land and tundra vegetation, both with a higher winter albedo than tall deciduous shrubs which are assumed to be taller than the depth of the winter snowpack. The decline in shrub cover is a result of warmer summers and a slight decline in annual precipitation over the period. A slight increase in cloudiness from the mid-1980s results in lower incoming photosynthetically active radiation, reducing photosynthesis. The resulting combination of changes leads to less plant-available soil water, greater autotrophic respiration, and a reduction in both GPP and NPP that causes shrubs to decline, but favours ground vegetation due to the reduced shading by shrubs.

Figure 6 summarises the broad mechanism leading to the reduction in regional winter albedo seen in Fig. 5 and in Table 1. Regionally, rising temperatures and increasing precipitation in the region from 1980 (Fig. 3c, d) lead to simulated increase in the coverage of tall vegetation, particularly shrubs (Fig. 4). The result is a reduction in albedo over much, though not all (Fig. 5) of the study domain.

DISCUSSION

Our simulation results suggest that the pan-Arctic tundra biome should exhibit increased productivity in response to an overall warming trend over the period 1980–2006 (Fig. 3). The main mechanism behind the productivity increase is a temperature-dependent advancement of the spring onset of photosynthesis, leading to a longer growing season. Plants invest part of their additional production in a higher leaf area and in horizontal and vertical canopy growth, increasing light interception and further

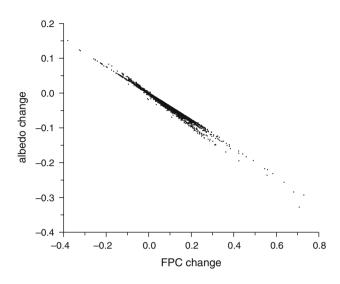


Fig. 6 Change in winter albedo 1983–2006 in relation to change in summed fractional projective cover (FPC) for tree and shrub PFTs. *Points* correspond to grid cells of the study domain

augmenting production. The simulated productivity increase is consistent with results from tundra warming experiments (Michelsen et al. 1996; Arft et al. 1999; Graglia et al. 2001; Walker et al. 2006; Olsrud et al. 2010), and productivity trends inferred from satellites (Bunn and Goetz 2006; Beck and Goetz 2011), while the increase in LAI is consistent with a positive trend in remotely sensed NDVI across the Arctic tundra biome over the same period (Fig. 3; Bhatt et al. 2010). Changes in community or landscape structure also emerged from the simulations. In one representative grid cell (Fig. 5), coverage by tall shrubs increases at the expense of dwarf shrubs, herbs and mosses, while the non-vegetated fraction of the grid cell declines. The underlying mechanism in the model is an increase in light attenuation, favouring taller plants to the detriment of the ground vegetation they shade. Shrub expansion and densification has been reported in numerous studies and related to recent warming trends (Kullman 2002; Jia et al. 2003; Tømmervik et al. 2004; Tape et al. 2006; Hedenås et al. 2011; Rundqvist et al. 2011). A popular hypothesis is that increased microbial activity in warmer soils enhances the availability of nutrients, particularly nitrogen, and that this lends a competitive advantage to shrubs relative to other types of tundra plants (Chapin et al. 1995; Tape et al. 2006). This temperature-nutrient effect cannot explain the simulated increase in shrub abundance in LPJ-GUESS, as the model does not include nutrient cycling; community

changes in our study are primarily mediated by increased competition for light as the productivity and density of vegetation increases.

Elmendorf et al. (2012) analysed changes in community structure at 158 tundra vegetation plots spread over much of the Arctic (excluding Russia), surveyed between 1980 and 2010. Consistent with our simulations, a significant proportion of plots showed increase in plant canopy height, an increased overall abundance of shrubs and decreased coverage of bare ground; these trends could be explained by increasing summer temperatures. However, trends for deciduous shrubs, herbs and mosses were less homogeneous, exhibiting both negative and positive trends at different locations, some of this variability being attributable to inter-site differences in moisture, presence or absence of permafrost, and the baseline temperature regime of the site; for example, deciduous shrub cover increased with warming in (colder) high-Arctic sites, but decreased with warming in low-Arctic sites (Elmendorf et al. 2012).

The simulated vegetation changes, particularly an increased fractional cover of tree and shrub PFTs, resulted in a decline in both winter and summer albedo from 1983 to 2006 (Figs. 5, 6; Table 1). The winter albedo decline of 1.75 % averaged over the study domain is, as expected, more marked, and may be compared with an average albedo reduction of 6 % estimated for the Barents Sea Region under an SRES-B2 future climate scenario by Wolf et al. (2008a), or a 5 % decline (May) when present-day vegetation fields in the HIRHAM regional climate model were replaced by LPJ-GUESS-simulated forest cover under an A1B future climate scenario (Matthes et al. 2012). Locally, the computed winter albedo changes in our study ranged down to -10 to 30% (Figs. 5, 6). The largest changes correspond to areas where the model is simulating a poleward advancement of the taiga-tundra boundary, or a marked increase in tree or shrub cover, in response to warming (Fig. 6). Similarly, in a future climate study with a regional Earth system model (Wramneby et al. 2010), warming-driven advancement of the elevational treeline in the Scandinavian mountain range reduced winter albedo by some 15 %, effecting a 0.2-0.5 °C increase in simulated winter warming-a positive feedback to climate. How significant might albedo feedbacks be compared with the radiative forcing of rising greenhouse gas concentrations? Bonfils et al. (2012) examined the effect of replacing modern vegetation fields in the CCSM4 GCM with scenarios in which much of the present-day tundra zone of the Arctic is populated with a dense coverage of short or tall deciduous shrubs. Tall shrubs (2 m height) were assumed to protrude from snow cover, reducing reflectance of incoming radiation throughout the year, while short (0.5 m)shrubs could be masked by snow for part of the year, depending on local climate and snow pack dynamics. The addition of shrubs reduced the average albedo over land by up to ca. 10 % (short shrubs) or ca. 25 % (tall shrubs) in the late snow season. The albedo changes are accompanied by an increase in evapotranspiration and atmospheric moisture content that, in combination, result in an annual temperature increase of 0.66 °C (short shrubs) or 1.84 °C (tall shrubs), comparable in magnitude to a further increase in temperatures that results from doubling atmospheric CO_2 concentrations in an additional experiment with the same model (Bonfils et al. 2012).

Vegetation-mediated changes in albedo have already been documented (Chapin et al. 2005) and may be contributing to Arctic amplification of climate change. Experiments using Earth system models demonstrate that the associated feedbacks are positive and may well be large, so that failing to account for them in future climate studies may result in inaccurate projections. Vegetation dynamics and ecosystem carbon cycling are now being incorporated in many climate models. For the case of the Arctic it will be important to adopt vegetation dynamics parameterisations that adequately reflect the response mechanisms of Arctic plant types and communities to climate change. The Arctic version of LPJ-GUESS employed in this study is being developed for this purpose.

Callaghan et al. (2011) challenged modellers to test the ability of their tools to reproduce trends and variations in tundra ecosystems seen in monitoring studies. We have accepted the challenge, and to some extent LPJ-GUESS proved successful in simulating the enhanced productivity and increased woody component in vegetation, apparent in many observational studies, and attributable at least in part to a positive temperature trend over the Arctic since the 1970s (see discussion and references above).

At a detailed level, there are still discrepancies and shortcomings in the modelling, and many open questions as to the mechanisms behind the real-world ecosystem changes. One important issue concerns nutrient cycling, believed to play a key role in the observed community changes, but not yet included in the Arctic version of LPJ-GUESS (nitrogen cycling is now included in the more generalised global version of the model). A further issue concerns the heterogeneity of responses seen in different studies and in different parts of the Arctic (e.g. Callaghan et al. 2011; Elmendorf et al. 2012). While temperature regimes are obviously a major driver of ecosystem structure and function in polar regions, other factors such as water balance, geology, soil type, trophic interactions, as well as anthropogenic management and land use also play an important role, and in some situations the combination of several drivers may lead to 'counterintuitive' changes, even over a period when temperatures are rising consistently and markedly.

To some extent a process-based model can be an excellent tool for studying the combined impacts of

multiple drivers. This is illustrated by the fact that LPJ-GUESS simulated reductions in shrub cover in some parts of the Arctic in the present study, as a result of a negative precipitation trend superimposed on rising temperatures. However, a large-scale model can only represent those processes and mechanisms that (a) are sufficiently well-understood to be represented in a quantitative way and incorporated in the model, and (b) for which the *drivers* are sufficiently well-observed to be upscaled and provided as input data across the domain of application of the model. Fulfilling both conditions and enhancing the ecological realism of ecosystem models in general is dependent upon a concerted effort on the part of empirical researchers to continue to refine understanding of key mechanisms, and to map relevant variables along geographic gradients. Through a wealth of in-depth ecological studies, coordinated experimental networks and synthesis initiatives like the Arctic Climate Impact Assessment (ACIA 2005) and the International Polar Year-Back to the Future Project (Callaghan et al. 2011), the Arctic research community has been active in providing modellers with the data they need, in the form they need it. We judge that the prospects for developing competent models of vegetation responses to climate change in the Arctic are good.

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