Shifts in Arctic vegetation and associated feedbacks under climate change

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Climate warming has led to changes in the composition, density and distribution of Arctic vegetation in recent decades[1-4]. These changes cause multiple opposing feedbacks between the biosphere and atmosphere[5-9], the relative magnitudes of which will have globally significant consequences but are unknown at a pan-Arctic scale[10]. The precise nature of Arctic vegetation change under future warming will strongly influence climate feedbacks, yet Earth system modelling studies have so far assumed arbitrary increases in shrubs (for example, +20%; refs 6,11), highlighting the need for predictions of future vegetation distribution shifts. Here we show, using climate scenarios for the 2050s and models that utilize statistical associations between vegetation and climate, the potential for extremely widespread redistribution of vegetation across the Arctic. We predict that at least half of vegetated areas will shift to a different physiognomic class, and woody cover will increase by as much as 52%. By incorporating observed relationships between vegetation and albedo, evapotranspiration and biomass, we show that vegetation distribution shifts will result in an overall positive feedback to climate that is likely to cause greater warming than has previously been predicted. Such extensive changes to Arctic vegetation will have implications for climate, wildlife and ecosystem services.

Vegetation productivity in Arctic ecosystems has increased over the past few decades, resulting in a trend of greening that is coincident with increases in Arctic surface air temperatures, which have risen at approximately twice the global rate[12]. Continued greening over the next century will produce multiple climate feedbacks. For instance, expansion of woody shrubs and trees into the tundra biome will act as a positive feedback to climate warming through increased surface net short-wave radiation associated with reductions in albedo due to taller and darker canopies[5]. Higher rates of evapotranspiration associated with woody vegetation will increase atmospheric water vapour concentrations, causing a second positive feedback to regional atmospheric heating[6,8]. Locally, shading associated with increasing shrub canopy cover may reduce soil temperatures, potentially slowing carbon release due to permafrost degradation and thus acting as a negative feedback to climate warming[7].

We estimate the influence of future climate-change predictions on the distribution of Arctic vegetation types using machine-learning, multi-class, ecological niche models[13] implemented at relatively fine spatial resolution (4.5 × 4.5 km cells) and with Arctic

Table 1 | Vegetation classes used in the models.

Vegetation class	Code	Area (km²)
Rush/grass, forb, cryptogam tundra	G1	137,781
Graminoid, prostrate dwarf-shrub, forb tundra	G2	427,376
Non-tussock-sedge, dwarf-shrub, moss tundra	G3	566,190
Tussock-sedge, dwarf-shrub, moss tundra	G4	335,462
Prostrate dwarf-shrub, herb tundra	P1	396,536
Prostrate/hemiprostrate dwarf-shrub tundra	P2	138,551
Erect dwarf-shrub tundra	S1	687,224
Low-shrub tundra	S2	611,307
Tree-cover mosaic	T1	200,536
Tree cover	T2	204,363

Areas for non-tree classes are within the study domain defined by the Circumpolar Arctic Vegetation Map (CAVM; ref. 30). As tree classes T1 and T2 do not extend into the CAVM region at present, areas shown for those classes are within the calibration buffer, which extends 100 m due south around the CAMV (Methods).

vegetation resolved into four classes of graminoids, four classes of shrubs and two classes of tree cover (Table 1). The models use statistical associations between present biotic distributions and abiotic variables to define characteristic niches for each plant type[13]. We used explicit multi-class likelihood to define niches in the presence of competition from all other vegetation types. Niche models are especially well suited to application in the Arctic owing to the strong role of abiotic factors in determining species' distributions in these harsh environments[14]. Comparison of observed and modelled vegetation classes under present climate revealed strong predictive performance, although use of a space-for-time test showed a decline in performance as models extrapolate further across space, and by extension across time (Supplementary Information).

Whereas our approach for predicting future vegetation distribution relies on statistical associations rather than biological mechanisms, process-based Earth system climate models with dynamic vegetation have also been developed and applied in the Arctic and boreal regions[2]. Process-based models generally operate at very coarse spatial resolutions (for example, half-degree)[15], focus on a subregion[16], or do not provide spatially explicit predictions of shifts in vegetation types[17]. Process-based models also may not adequately incorporate all processes or plant functional types that influence vegetation-climate feedbacks in the Arctic[18]. In particular,

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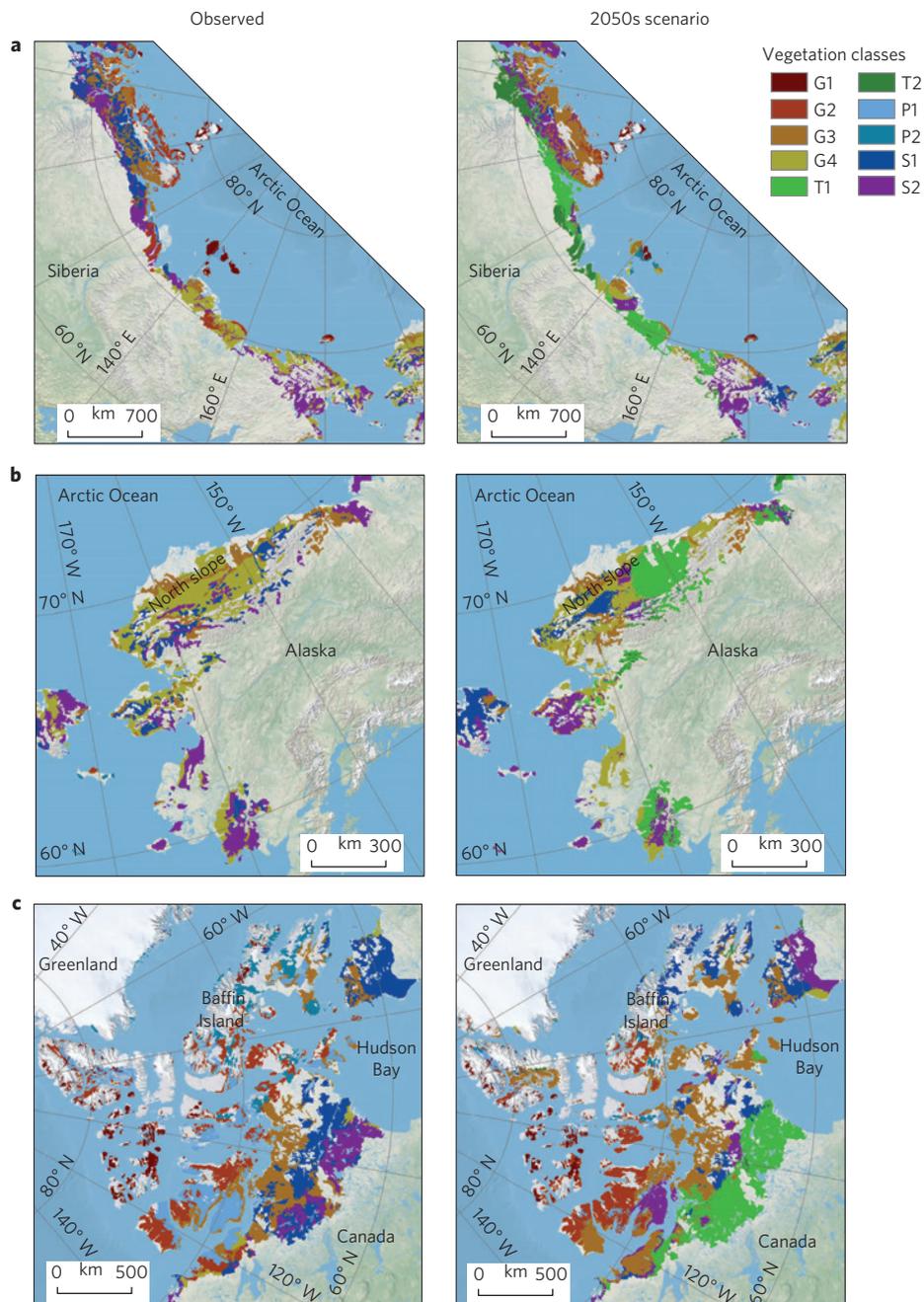
Figure 1 | Observed and predicted distributions of vegetation. Observed distributions of vegetation classes (left) and predicted distributions for the 2050s based on an equilibrium dispersal scenario (unrestricted colonization of trees), Random Forest model, HadCM3 AOGCM, and A2a emissions scenario (right). **a**, Siberia. **b**, Alaska. **c**, Western Canada. Modelled vegetation classes are overlaid on a physical terrain map (US National Park Service). Projection: Lambert azimuthal equal area.

Arctic vegetation is commonly resolved into too few categories to include some plant types that are thought to have important physical and biogeochemical implications for the climate system, including mosses, lichens and deciduous shrubs[19]. As process-based representations of vegetation dynamics continue to improve, statistical ecological niche models provide a valuable parallel approach.

We find that vegetation in 48–69% of our study area is predicted to shift to a different physiognomic class under scenarios of restricted tree dispersal and climate change for the 2050s (Supplementary Methods). As much as 57–84% of the area is predicted to shift to a different class under an equilibrium scenario with unrestricted dispersal, which is supported by evidence of rapid shifts to larger growth forms due to phenotypic variation[4] and rapid colonization due to long-distance dispersal[20], expansion from isolated refugia[21], and favourable conditions for establishment following large tundra fires[22] and thermokarst related to permafrost thaw[23]. Such widespread redistribution of Arctic vegetation (Fig. 1 and Supplementary Fig. S2) would have impacts that reverberate through higher trophic levels[24], affecting wildlife and ecosystem services that are important for human well-being, including food production, access to natural resources, and traditional cultural identity[25]. These impacts would extend far beyond the Arctic region owing to effects on species that seasonally migrate from lower latitudes and rely on finding particular polar habitats, such as open space for ground-nesting birds[26].

The equilibrium scenario shown in Fig. 1 illustrates the potential for massive expansion of tree cover, including across much of northern Siberia, as climate becomes suitable for tree growth sometimes hundreds of kilometres north of the present tree line. In many areas, including on Alaska's North Slope, erect dwarf-shrub tundra (class S1) and low-shrub tundra (class S2) are predicted to encroach into landscapes dominated by graminoids at present. In other areas, prostrate shrubs are predicted to be replaced by erect shrubs; for instance, in the southern half of Baffin Island prostrate dwarf-shrub, herb tundra (class P1) is predicted to become erect dwarf-shrub tundra (class S1; Fig. 1). Although these trends are largely consistent across alternative models and scenarios, the choice of atmosphere–ocean general circulation model (AOGCM) and machine-learning algorithm does affect the results (Supplementary Fig. S2) and fine-scale results for a particular scenario should not be interpreted as precise predictions. Moreover, there are other positive feedbacks associated with shrub expansion that we have not accounted for, including local soil warming and increases in nutrient availability[27]. These factors will lead to an underestimation of woody vegetation expansion, offsetting factors that could affect predictions in the opposite direction, such as time lags associated with growth and recruitment. However, although the model results are likely to differ from realized outcomes in detail, the models provide useful estimates of broad-scale trends and the likely magnitude of change over the coming century.

Considering changes in the area covered by each class, summarized across all alternative models and scenarios (Fig. 2 and Supplementary Table S3), we predict large contractions for some vegetation classes. Risk of extinction will be increased for species found within classes that contract. In general, distributions of lower-lying vegetation classes with sparse plant cover are predicted to contract as larger shrubs and trees expand their ranges; however, the spatial configuration of high-latitude land masses complicates this general trend. For instance, tundra vegetation dominated by tussock sedge, dwarf shrub and moss (class G4) is predicted to contract despite having the tallest plants and densest coverage of the four graminoid classes considered (Fig. 2). This class is mostly restricted to Alaska, Siberia and north-eastern Russia, which are regions that do not have more northerly land masses to which vegetation could shift as trees and larger shrubs immigrate from the south (Fig. 1).

To explore the implications of these findings for biosphere–atmosphere feedbacks, we estimated future changes in albedo, evapotranspiration and above-ground biomass (AGB) by calculating these variables per unit area for each vegetation class, based on satellite imagery, and then assigning them to projected distributions of vegetation classes (Supplementary Methods). As direct albedo is dependent on local solar zenith angle, we used broadband diffuse short-wave albedo (Supplementary Methods). We calculated mean annual albedo (α) to account for the combined effects of vegetation change and climate-induced increases in growing-season length on albedo. We also examined albedo for the month of May (spring albedo: α_S) to determine whether annual changes are associated with changes in growing-season length or the snow-masking effects of vegetation. Here, small changes in α_S indicate that changes in α are dominated by changes in growing-season length, whereas larger changes in α_S correspond to effects of vegetation over snow. Further, we calculated surface net short-wave radiation (S_N) by multiplying monthly incident short-wave radiation by monthly albedo and then taking the mean of monthly S_N to arrive at an annual value. Changes in S_N and evapotranspiration serve as an indication of the extent to which projected vegetation changes will have a quantifiable effect on pan-Arctic surface energy budgets (Supplementary Methods).

We estimate that α will decrease by 2–5% (from 0.455 to 0.430–0.447) under restricted tree dispersal, and by 7–18% (to
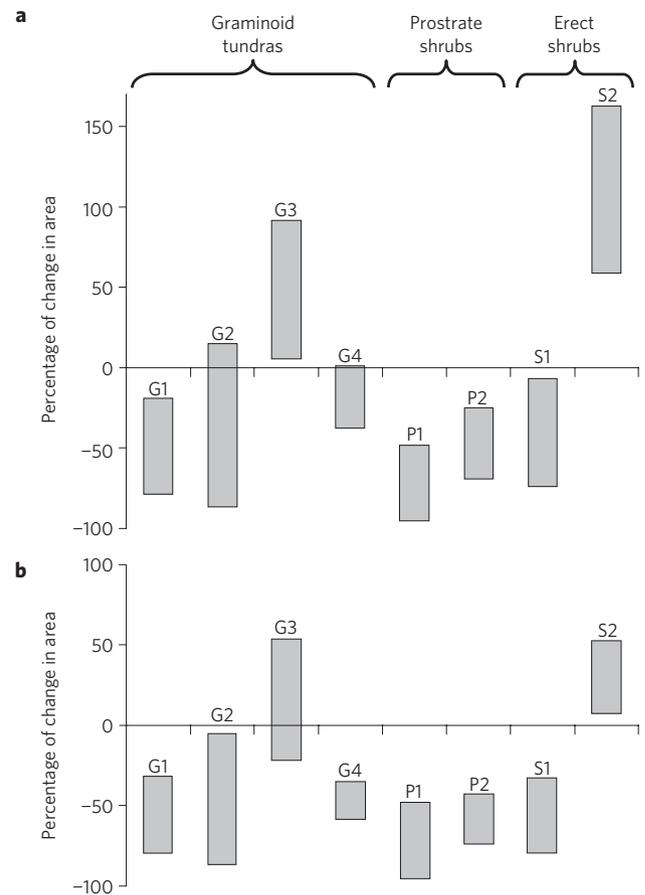
Figure 2 | Predicted changes in area by vegetation class for the 2050s. **a**, Restricted tree dispersal scenarios. **b**, Equilibrium scenario (unrestricted colonization of trees). Grey bars show the range of predictions due to alternative machine-learning models, AOGCMs, emissions scenarios and dispersal scenarios. Tree classes are excluded from this figure because they have no present-day coverage within the study region, so relative changes in area cannot be calculated.

0.374–0.422) under equilibrium; α_S is predicted to decrease by 2–6% (from 0.664 to 0.623–0.653) under restricted tree dispersal, and by 10–26% (to 0.491–0.595) under equilibrium. These changes are largely due to the snow-masking effects of taller vegetation, indicating that the projected vegetation changes would exacerbate rates of regional warming that are already amplified. Changes in α correspond to increases in S_N of 1.07–3.11 W m^{-2} under restricted dispersal and 3.54–8.71 W m^{-2} under equilibrium. Monthly values of projected S_N change illustrate a shift in both the timing and magnitude of the maximum monthly contribution to annual S_N, with greater increases in S_N occurring earlier in the year under equilibrium relative to restricted dispersal scenarios (Fig. 3). Although temperature-induced increases in growing-season length have dominated the Arctic snow-albedo feedback in recent decades[28], this finding illustrates that the contrast between spring and summer albedo will be increasingly important over the coming century. Our results underscore the need to characterize albedo during snow-covered to snow-free transitions alongside increases in growing-season length in future work to quantify albedo feedbacks at high latitudes in coupled climate models.

Evapotranspiration is predicted to increase by 1–4% by the 2050s (from 15.62–15.63 to 15.75–16.19 W m^{-2}) under restricted tree dispersal, and by 5–13 % (to 16.46–17.73 W m^{-2}) under equilibrium considering the effect of changes in vegetation type

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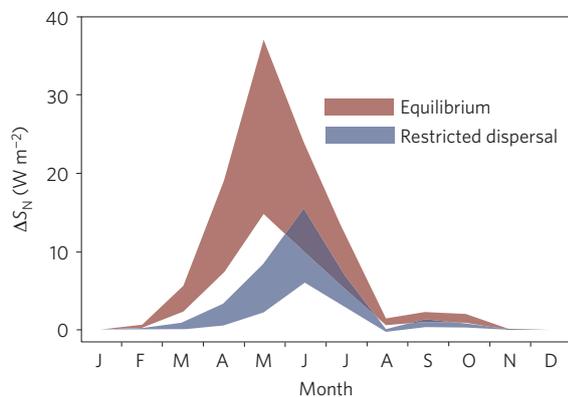
Figure 3 | Predicted monthly changes in surface net short-wave radiation for the 2050s. Red shading shows the range of predicted changes in monthly S_N across machine-learning models, AOGCMs and emissions scenarios under equilibrium (unrestricted tree dispersal scenario). Blue shading shows the range of predicted changes in monthly S_N across machine-learning models, AOGCMs and emissions scenarios under restricted dispersal. Note that changes in S_N are driven solely by albedo as incident short-wave radiation is held constant.

alone. These predicted increases in evapotranspiration are relatively small, with increases for the restricted dispersal scenario ($0.13–0.56\,W\,m^{-2}$) comparable to estimates of increases associated with observed changes in growing-season length in recent decades[29]. Under equilibrium conditions, projected increases in evapotranspiration are larger ($0.84–2.10\,W\,m^{-2}$), but still small relative to the predicted increases in S_N, suggesting that albedo will dominate climate feedbacks associated with changes in surface energy budgets.

AGB is predicted to increase by 15–42% by the 2050s (from 1.85–1.86 to 2.13–2.64 Pg) under restricted tree dispersal, and by 29–68% (to 2.39–3.13 Pg) under equilibrium. Our maximum predicted total increase in AGB under equilibrium for 2050s climate scenarios (1.27 Pg phytomass) is roughly equivalent to the projected annual efflux of soil carbon to the atmosphere as a consequence of permafrost thaw over the coming century ($0.8–1.1\,Pg\,C\,yr^{-1}$; ref. 9). The total radiative forcing associated with this increase in biomass under equilibrium for 2050s is between -0.003 and $-0.008\,W\,m^{-2}$. These values are again small in comparison to annual changes in S_N and evapotranspiration. These predictions reinforce that although Arctic soils are a carbon reservoir of global significance, vegetation in the Arctic affects climate primarily as a biophysical medium.

Considering vegetation classes that are likely to induce a biophysical state shift, we predict that woody shrubs (class S2) and trees (classes T1 and T2) will expand to cover a further 12–33% of the study domain under restricted tree dispersal, and 24–52% under equilibrium. Two recent climate modelling studies employed an arbitrary increase in shrub cover of ∼20% to represent potential conditions in the year 2100 (refs 6,11) and concluded that regional warming (as a result of albedo and evapotranspiration feedbacks) will be strong enough to counteract the local cooling effects of increased canopy cover on soil temperatures, thereby producing regional warming of 0.66–1.8 °C and increased active layer depth of ∼10 cm. Our results suggest that the assumptions underlying these predictions are realistic but may be realized much sooner than 2100 (on the basis of our restricted dispersal results for 2050s) and may substantially underestimate the areal expansion of shrubs (if our equilibrium scenario is approached by 2100). The contribution of albedo and evapotranspiration feedbacks to continued Arctic warming over the twenty-first century is therefore likely to be greater than expected at present. Amplified regional warming as a consequence of these feedbacks will probably mean that feedbacks associated with carbon mobilization due to permafrost thaw will also be stronger.

Methods

The study domain is defined by the Circumpolar Arctic Vegetation Map[30] (CAVM), which was derived from Advanced Very High Resolution Radiometer (AVHRR) imagery extending south as far as the northern limit of forest cover. The eight tundra vegetation types that we model are based on classes of dominant vegetation physiognomy used in the CAVM (Table 1). To allow simulations of forest cover moving northward into the study domain under future climate warming, we set a buffer extending 100 km due south around the domain for model calibration. Two classes of forest cover mapped from the Global Land Cover 2000 database were used to calibrate the models within the buffer (Table 1 and Supplementary Methods).

We used 19 bioclimate variables from the WorldClim database, as well as a variable characterizing substrate chemistry, to drive the models. Future climate scenarios were based on three AOGCMs (CCCMA, HadCM3, CSIRO) downscaled to very high resolution, and high- and low-emissions scenarios (Intergovernmental Panel on Climate Change Special Report on Emission Scenarios A2a and B2b, respectively) up to the 2050s. We applied two multi-class machine-learning approaches—Random Forests and multi-class multi-kernel Relevance Vector Machines. For tree classes under the restricted dispersal scenarios, we applied minimum and maximum expected dispersal distances of 5 and 20 km by the 2050s, based on observed rates of treeline displacement at northern high latitudes (Supplementary Methods).

We used composites of MODIS data for the years 2001–2010 to calculate changes in albedo and evapotranspiration. Incident short-wave radiation used to calculate S_N was generated for the years 2001–2003. Biomass was mapped by the CAVM team[30] by calculating the Normalized Difference Vegetation Index (NDVI) from AVHRR data and then transforming NDVI to AGB on the basis of calibration with *in situ* harvest data. Biomass was converted to atmospheric CO_2 equivalent to calculate the associated radiative forcing (Supplementary Methods).

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Author contributions

R.G.P. and S.J.G. conceived the study; R.G.P. analysed data; S.J.P. analysed data and ran Random Forests models; M.M.L. led albedo and evapotranspiration analyses; P.S.A.B. led biomass and S_N analyses; T.D. ran multi-kernel Relevance Vector Machines models; S.J.K. ran preliminary analyses; R.G.P., M.M.L. and P.S.A.B. wrote the paper with contributions from all authors.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to R.G.P.

Competing financial interests

The authors declare no competing financial interests.