Citizen science predicts the distribution of pine trees in the Fennoscandian Arctic

Juan Ignacio Ramirez[1]

[1]Umeå University

December 5, 2023

Abstract

The effects of climate change in the Arctic are particularly pronounced since temperatures have risen nearly three to four times as fast as in the rest of the planet. Shifts in climatic patterns enable the expansion of temperature-limited vegetation at a global scale to higher latitudes and elevations. The purpose of this study is to predict the distribution of pine trees (*Pinus sylvestris*) across Fennoscandia by drawing from three distinctive datasets. I ask (i) How will the distribution of pine trees will respond to climate change in the next 50 years? (ii) Which method used to collect data is better at predicting the distribution of pine? Three datasets on pine presence together with environmental data were used to model pine distribution with Generalized Linear Models. The first dataset belongs to the Swedish National Forest Inventory and the second is from a Swedish online portal where citizens report their observations of species. The third was compiled by setting up a network of vegetation plots along an elevation gradient in Sweden and Norway. Current and future environmental data was sourced from the Coupled Model Intercomparison Project. The probability of pine presence in general increased with temperature and decreased with precipitation. Therefore, the model forecasts that pine will expand in distribution to areas of higher elevation. The citizen science dataset was superior in predicting pine distribution due to the large number and the wide spatial distribution of observations. The conservation of the tundra and the unique ecosystem process taking place in this area will be threatened by the encroachment of the evergreen treeline which is driven by climate, and citizen science holds unique importance for wide spatial and temporal ecological research.

Keywords

Arctic; Climate Change; Ecotone; Forest; Global Change Ecology; Species Distribution Model

Introduction

The effects of climate change in the Arctic are particularly prominent, as temperatures have risen nearly three to four times as fast as in the rest of the planet (Field & Barros, 2014; Rantanen et al., 2022; Zhu et al., 2016). Shifts in climatic patterns enable the expansion of temperature-limited shrub vegetation at a global scale to higher latitudes and elevations (Asmus et al., 2018; Myers-Smith et al., 2020; Sweet et al., 2015). This phenomenon is not only particular to shrubs but also to treelines that occur at the edge of the forest-tundra habitat, where temperature-limited trees are barely capable of growing. Treelines shadow climate patterns by expanding or shrinking their distribution across large spatial scales to ensure optimal abiotic and biotic conditions to develop (Dial et al., 2022; MacDonald et al., 1993; Reich et al., 2022). Warmer temperatures release the nutrients trapped in cold soils, allowing optimal establishment and development of trees (Hobbie & Chapin, 1998; Sullivan et al., 2015). Treelines are expanding in range across the planet due to warmer ambient temperatures (Holtmeier & Broll, 2005; Kruse et al., 2019; Pearson et al., 2013; Rees et al., 2020; Rupp et al., 2001). The response of treelines to climate change is tree species-specific, since the set of traits particular to each tree species is what determines its ability to establish, develop, reproduce, and disperse to novel sites. Studies in Fennoscandia however have forecasted the distribution of broadleaf trees and overseen the distribution of conifer trees (Rees et al., 2020).

The treelines in Fennoscandia consist mainly of birch (*Betula pubescens*) and in less proportion of pine (*Pinus sylvestris*) or spruce (*Picea abies*) and occasionally mix-species treelines are found (Kullman, 2002, 2007). The evergreen pine trees, the target species of this study, are generally known to have a unique set of traits that allows them to adapt to unique conditions such as saving energy during winter by not shedding their needles (Ottander et al., 1995), high plasticity in root architecture to secure water and nutrients in situations of drought and depleted soils (Moser et al., 2015) and possessing recalcitrant needles that are barely palatable for herbivores (Maes et al., 2019; Ramirez, Jansen, den Ouden, Moktan, et al., 2021). Pine trees on the other hand, cannot grow in shaded areas because they are light-demanding (Niinemets, 2010) and they have low tolerance to tissue damage by herbivores due to their strong apex shoot dominance (Aarssen, 1995). These set of unique traits allow pine trees to grow at their minimum temperature range while forming treelines in the Fennoscandian Arctic (Kullman, 2007). The extent to which pine trees will shift their spatial distribution as a response to future environmental conditions due to climate change remains largely unknown.

The purpose of this study is to predict the distribution of pine trees in the Fennoscandian Arctic by drawing from three datasets that implemented distinctive methods during data collection. This is done by employing three independent species distribution models (SDM), one for each of the datasets. The first dataset includes observations of the presence and absence of pine made only by me (a researcher) across an elevation gradient in four distinct locations in Sweden and Norway. The second dataset belongs to the Swedish National Forest Inventory and includes a wide network of permanent plots across Sweden to estimate forest metrics and track these metrics over time. The third dataset belongs to the Artdatabanken which is an online platform that gathers observations reported by citizens, nature officers, and researchers from across all regions in Sweden. Understanding the implications of how different data collection methods have on the predictions yielded by SDM provides researchers with the necessary input to choose the best experimental design for their study.

To address this research objective, I raised two questions: (i) How will the distribution of pine trees respond to climate change in the next 50 years? (ii) Which method used to collect data is better at predicting the distribution of pine trees as a response to climate change? (I) I predict that the pine distribution will only expand to higher elevations and latitudes as climate change releases the temperature limitation in pine performance. (ii) Citizen science data will be best suited to predict the distribution of pine trees because this method yields a greater number of observations that are distributed across an entire elevation gradient (Richardson & Whittaker, 2010). Although my dataset compiles pine observations along an elevation gradient, it falls short in the number of observations due to the limitation in manpower. The NFI compiles a great number of pine observations, but these do not cover the entire elevation gradient.

Methods

Study area

The study area covered the Fennoscandian peninsula, which includes Sweden, Norway, and Finland. The visual representation of the pine SDM includes other countries that need to be ignored since no data was collected in these territories.

Vegetation plot network

I walked along an elevation gradient at four sites in Sweden to establish a network of 5x5-meter vegetation plots to record the presence and absence of pine trees. Abisko, Jäkkvik, Nordli, and Ånn were chosen because they are among the few locations in Fennoscandia that harbor a treeline composed of birch and pine trees. Between the summer of 2020 and 2021, I carried out data collection by annotating the presence and absence of pine, and for each observation, I annotated the geographical coordinates. A minimum distance of 150 meters was used between observations to ensure an accurate representation of the true distribution of pine. This fieldwork campaign yielded a total of 195 data points unevenly distributed between the four locations: Abisko (n=77), Jäkkvik (n=37), Nordli (n=43), Ånn (n=38). This dataset is now referred to as PLOT.

Swedish National Forest Inventory

Sweden for the last 100 years has been systematically collecting and storing data to create an updated inventory of its forests. An extensive network of permanent plots with a size of 154 m^2 is used for the forest inventory (Fridman et al., 2014). For this project, I drew a subset of the official data by downloading the readily available file from the webpage of the Swedish University of Agricultural Sciences (`https://www.slu.se/nfi`) and filtering in data from the 2022 field survey (Swedish NFI, 2023). The presence and absence of pine trees were extracted from these data along with the geographical coordinates of the plot. This data extraction yielded a total of 2,356 data points. This dataset is referred to as NFI.

SLU Artdatabanken

The Swedish University of Agricultural Sciences administers the species the Swedish Species Observation System (Artportalen) to register and map the species diversity of Sweden. This is an online portal where citizens, conservationists, and researchers can report the species they have observed (`https://artportalen.se/`). I used a subset of this databank by filtering in data on pine and only for observations made between June 2nd of 2020 and June 2nd of 2023. The presence of pine trees was extracted from this dataset along with the geographical coordinates of the observations. This process yielded a total of 9359 data points. Since these data do not include the absence of pine trees, I merged the absence data from the PLOT network into this dataset (n=71). From now on, this dataset is referred to as ART.

Environmental data

Current and forecast global environmental data in the form of minimum temperature (K) and annual precipitation (kg m^{-2} s^{-1}) was sourced from Coupled Model Intercomparison Project phase 5 (i.e., the CMIP5 multi-model ensemble data, `https://esgf-node.llnl.gov/projects/esgf-llnl/`). This project developed a scientific framework that yielded likely estimates of environmental data linked to GPS coordinates (Meehl et al., 2009; Taylor et al., 2012). The data used for this project belong to the 50-year forecast data library and these data are extensively used for the Intergovernmental Panel on Climate Change Assessment Reports (Appendix 1, Fig. S1.1). CMIP5 was favored over CMIP6 because its estimates are in line the observations, while CMIP6 robustness remains to be tested due to its recent release (Carvalho et al., 2022).

Data analysis

Generalized Linear Models (GLM) were used for understanding how environmental variables can be used to predict the current distribution of pine trees in western Fennoscandia. The spatial extent of the model includes Norway, Sweden and north Finland, while the temporal extend is the year 2023 for the current predictions and 2073 for the forecast. Three independent GLMs with a binomial and logit link function were specifically used to test the current pine distribution (presence vs. absence) set as a response to temperature (min) and precipitation as fixed factors sourced from the CMIP5 data. Each of the GLMs employed three distinct datasets (PLOT, NFI, ART). An interaction between temperature and precipitation was also tested, but it was omitted from this study because it did not improve the fit of the model. The fit of the model was evaluated by comparing the AIC values. The model diagnosis was done by assessing the spread of the residual and by plotting a Receiver Operator Characteristic Curve (ROC), both tools widely used in SDM (Miller, 2010; Zurell et al., 2020). The area under the ROC curve (AUC) was also extracted, which indicates the efficiency of the model to predict. The value ranges between 0 and 100, with 100 being a highly accurate model. A p-value < 0.05 was used as the threshold for a significant relationship between response and predictors. The forecast of the pine distribution was made by extrapolating to a map of Fennoscandia the three GLM responses linked to the future environmental data sourced from CMIP5. The AUC and the coefficient of determination was used to rank the models with distinct data collection methods. All statistical analysis was conducted in "R 4.0.2" (R Core Team, 2013). Maps and figures were done in "R" with the packages "ggplot2" version 3.3.5 and "ggmap" version 3.0.0.903 (Kahle & Wickham, 2013; Wickham & Winston, 2016).

Results

The probability of current pine presence responded positively with temperature (b=0.046, p=0.005, Table 1) and negatively with precipitation (b=-0.051, p<0.001) when employing the dataset belonging to the PLOT network. The probability of current pine presence responded negatively to temperature (b=-0.007, p<0.001) and precipitation (b=-0.020, p=0.009) when employing the NFI data. Finally, the probability of current pine presence responded positively to temperature (b=0.199, p<0.001) and negatively to precipitation (b=-0.192, p<0.001). See Table 1 for AUC and R^2 values and Appendix 1, Fig. S1.2 for ROC curves. When spatially forecasting with the PLOT and ART datasets, the pine distribution will likely expand in range to higher elevations and remain the same in lowland Fennoscandia (Fig. 1).

Table 1. Generalized Linear Model for the likelihood of having pine trees as a response to current temperature (min) and precipitation. The results for three identical models, one for each dataset type, are presented. The models are accompanied by the coefficient of determination (R^2), intercept, coefficients, and p-values.

Data	Response	AUC	R^2	Intercept	p value	Temp.	p value	Precip.	p-value
Plot	Pine	0.657	0.09	3.070	<0.001	0.046	0.005	-0.051	<0.001
NFI	Pine	0.561	0.02	1.306	<0.001	-0.007	<0.001	-0.020	0.009
ART	Pine	0.992	0.63	10.854	<0.001	0.199	<0.001	-0.192	<0.001

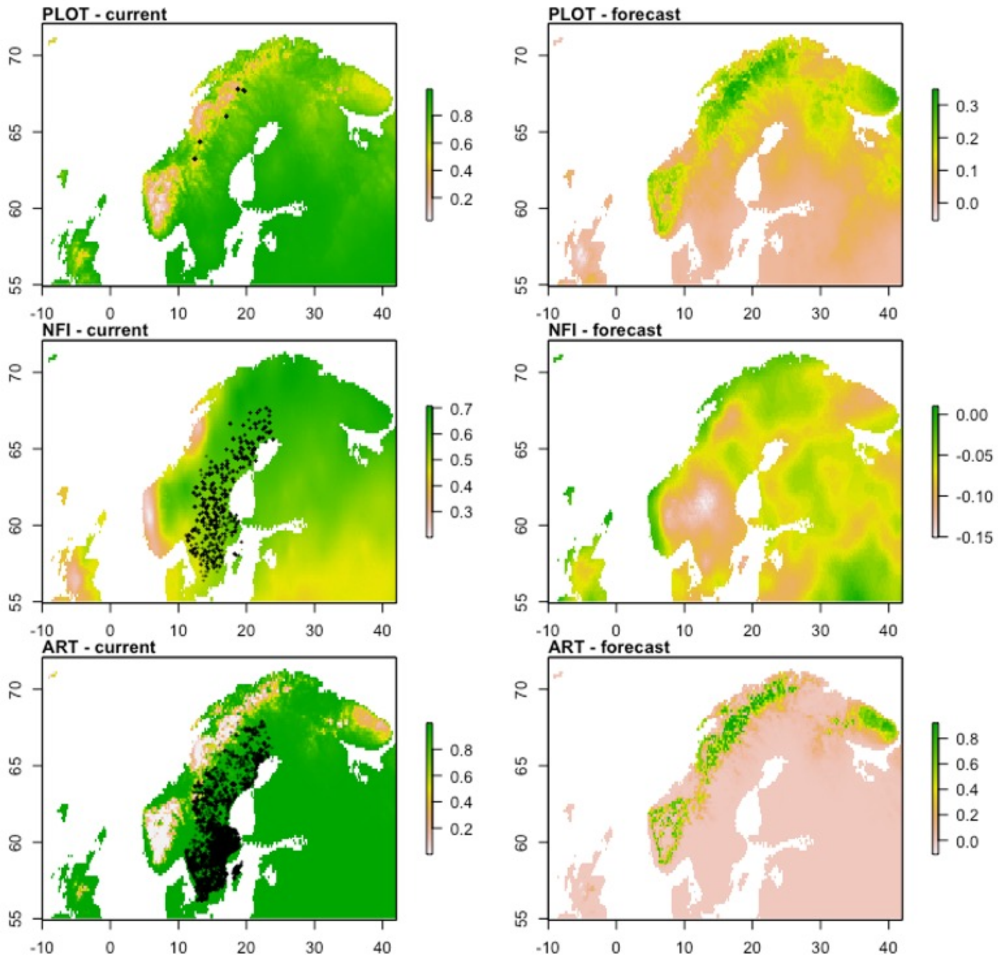

Figure 1: This is a caption

Figure 1. Graphical representation of the current distribution of pine trees in Fennoscandia (left column) and the 50-year forecast distribution of pine trees (right column). Black dots indicate individual observations used to model the pine distribution. The color gradient in the left column indicates the current likelihood of pine presence whereas the column to the right indicates the likelihood of variation when contrasting the current and the 50-year forecast for the presence of pine.

Discussion

The current distribution of pine trees across Fennoscandia was predicted as a response to current temperature and precipitation by employing GLMs. The models' responses were then used to forecast the distribution of the pine trees using future environmental data. The same procedure was repeated three times with distinct datasets to understand which methodology used to collect data is better for predicting the spatial probabilities of pine. The probability of pine presence overall increases with temperature and decreases with precipitation. Therefore, the model thus forecasts that pine will expand in distribution to areas of higher elevation. The dataset sourced by citizen sciences was superior in predicting pine distribution.

The distribution of pine will expand to higher elevations

With future changes in temperature and precipitation patterns, it is expected that pine will maintain its distribution in lowland Fennoscandia, but the likelihood of having pine trees at high elevations in the Scandes will increase. These specific areas should have no light limitation in the understory, present an increase in temperature, and should remain relatively dry for pine to thrive (Moser et al., 2015; Niinemets, 2010). The current pine treelines present an island-like shape rather than a continuous shape, and therefore I expect pine will continue to expand abruptly, where one or several outposts of a pine population establish and develop at a higher elevation (Harsch & Bader, 2011). This patchy distribution will depend on the current facilitation and dieback processes remaining in the future (Wiegand et al., 2006). These future shifts in pine distribution imply that the associated food web of the treeline will likely shift in distribution as well. This shift in community composition can lead to cascading effects on important ecosystem processes (Schleuning et al., 2015) taking part in the Arctic like primary productivity (Reich, 2014), carbon storage (Manning et al., 2015), nutrient cycling (Lavorel & Garnier, 2002) and evapotranspiration (Beringer et al., 2005).

The previous result is confirmed by experiments conducted in this region where Open Top Chambers (OTCs), which simulate an increase in ambient temperature, facilitate the establishment and development of shrubs and trees outside their usual niche boundaries (Arft et al., 1999), but also modulate the composition of other associated biodiversity such as invertebrates, mosses, and lichens (Dollery et al., 2006; Elmendorf et al., 2012; Sjursen et al., 2005). The expansion of the treeline not only responds to climatic patterns or so-called bottom-up control but also to top-down control. In this context, herbivory by large cervids plays a crucial role in the expansion of conifer treelines. Experimental work that set animal exclosures paired to a control plot in this same region confirms that herbivory limits the establishment and development of broadleaf and conifer trees on the treeline (Bognounou et al., 2018; Olofsson et al., 2001, 2009). The degree to which herbivory can limit the expansion of the treeline is dependent on the density of cervids and the composition since forest attributes decrease in a non-linear way with deer density (Ramirez, Jansen, den Ouden, Li, et al., 2021). The composition of the cervid guild, on the other hand, determines which vegetation type will more likely experience herbivory damage since deer species have different food preferences (Gill, 1992; Ramirez, 2021; Ramirez et al., 2023). Securing a large and diverse guild of cervids composed of browsers, intermediate feeders and grazers will likely maintain the current structure and composition of Arctic ecosystems by reducing the rate at which treelines are expanding across Fennoscandia (Olofsson & Post, 2018). Future studies can expand on treeline distribution –either at species or functional group level– by harnessing the results of this study and modeling it with other biological and environmental variables that shape treelines (Franklin, 2010; Midgley et al., 2006).

Citizen science is a powerful tool for SDM

Citizen science-based data (ART) were the most useful in predicting the distribution of pine trees in Fennoscandia followed by experimental data (PLOT) and forest data (NFI). The inherent characteristic of the large sample size and the fact that observations were done across the entire region in ART are the factors that improved the model output. Harnessing citizen science for broad spatial and temporal ecological research will yield a better understanding of environmental processes that researchers can only tackle in relatively large chunks of time (Dickinson et al., 2012). The Swedish government in this line has taken an important step by passing a bill in 2020 that strengthens citizen science as a tool for tackling environmental and sustainability challenges (Bína et al., 2021).

The PLOT dataset, although having a smaller sample size, was also efficient in predicting pine distribution probably because observations were planned according to a latitude and an elevation gradient that yielded a wide variation in temperature and precipitation patterns. This result implies that even when not possessing a large dataset on the presence and absence of targeted species, robust SDM can be constructed by planning a limited collection of data across environmental gradients where the species occur.

Conclusion

SDMs are imperative tools to identify current areas prone to changes in the structure and composition of their ecosystems when faced with future variations in temperatures and precipitation patterns. This study highlights that the pine distribution will likely expand towards higher elevations in Fennoscandia where pine trees are not currently present. Databases sourced from citizen science are extremely useful for the development of robust models that forecast the spatial distribution of species due to their large sample size and the wide environmental gradients where data are collected.

References

Aarssen, L. W. (1995). Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos*, *74*(1), 149–156. https://doi.org/10.2307/3545684

Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jónsdóttir, I. S., Laine, K., Lé Vesque, E., Marion, G. M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., … Wookey, P. A. (1999). Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, *69*(4), 491–511. https://doi.org/10.1890/0012-9615

Asmus, A. L., Chmura, H. E., Høye, T. T., Krause, J. S., Sweet, S. K., Perez, J. H., Boelman, N. T., Wingfield, J. C., & Gough, L. (2018). Shrub shading moderates the effects of weather on arthropod activity in arctic tundra. *Ecological Entomology*, *43*(5), 647–655. https://doi.org/10.1111/een.12644

Beringer, J., Stuart, F., Iii, C., Thompson, C. C., & Mcguire, A. D. (2005). Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agricultural and Forest Meteorology*, *131*(3–4), 143–161. https://doi.org/10.1016/j.agrformet.2005.05.006

Bína, P., Brounéus, F., Kasperowski, D., Hagen, N., Bergman, M., Bohlin, G., Jönsson, M., Coulson, S., & Hofmeester, T. (2021). Awareness, views and experiences of citizen science among Swedish researchers — two surveys. *Journal of Science Communication*, *20*(6), A10. https://doi.org/10.22323/2.20060210

Bognounou, F., Hulme, P. E., Oksanen, L., Suominen, O., & Olofsson, J. (2018). Role of climate and herbivory on native and alien conifer seedling recruitment at and above the Fennoscandian tree line. *Journal of Vegetation Science*, *29*(4), 573–584. https://doi.org/10.1111/jvs.12637

Carvalho, D., Rafael, S., Monteiro, A., Rodrigues, V., Lopes, M., & Rocha, A. (2022). How well have CMIP3, CMIP5 and CMIP6 future climate projections portrayed the recently observed warming. *Scientific Reports 2022 12:1*, *12*(1), 1–7. https://doi.org/10.1038/s41598-022-16264-6

Dial, R. J., Maher, C. T., Hewitt, R. E., & Sullivan, P. F. (2022). Sufficient conditions for rapid range expansion of a boreal conifer. *Nature*, *608*, 546–551. https://doi.org/10.1038/s41586-022-05093-2

Dickinson, J. L., Shirk, J., Bonter, D., Bonney, R., Crain, R. L., Martin, J., Phillips, T., & Purcell, K. (2012). The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, *10*(6), 291–297. https://doi.org/10.1890/110236

Dollery, R., Hodkinson, I. D., & Jónsdóttir, I. S. (2006). Impact of warming and timing of snow melt on soil microarthropod assemblages associated with Dryas-dominated plant communities on Svalbard. *Ecography*, *29*(1), 111–119. https://doi.org/10.1111/j.2006.0906-7590.04366.x

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., … Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, *15*(2), 164–175. https://doi.org/10.1111/j.1461-0248.2011.01716.x

Field, C. B., & Barros, V. R. (2014). *Climate change 2014–Impacts, adaptation and vulnerability: Regional aspects*. Cambridge University Press.

Franklin, J. (2010). Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, *16*(3), 321–330. https://doi.org/10.1111/J.1472-4642.2010.00641.X

Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Hedström, A., & Ståhl, G. (2014). Adapting national forest inventories to changing requirements–the case of the Swedish National Forest Inventory at the turn of the 20th century. *Silva Fennica*, *48*(3). https://doi.org/10.14214/sf.1095

Gill, R. M. A. (1992). A review of damage by mammals in north temperate forests: 1. Deer. *Forestry*, *65*(2), 145–169. https://doi.org/10.1093/forestry/65.2.145

Harsch, M. A., & Bader, M. Y. (2011). Treeline form – a potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, *20*(4), 582–596. https://doi.org/10.1111/j.1466-8238.2010.00622.x

Hobbie, S. E., & Chapin, F. S. (1998). An experimental test of limits to tree establishment in Arctic tundra. *Journal of Ecology*, *86*(3), 449–461. https://doi.org/10.1046/j.1365-2745.1998.00278.x

Holtmeier, F. K., & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, *14*(5), 395–410. https://doi.org/10.1111/j.1466-822x.2005.00168.x

Kahle, D., & Wickham, H. (2013). ggmap: spatial visualization with ggplot2. *The R Journal*, *5*(1), 144–161.

Kruse, S., Gerdes, A., Kath, N. J., Epp, L. S., Stoof-Leichsenring, K. R., Pestryakova, L. A., & Herzschuh, U. (2019). Dispersal distances and migration rates at the arctic treeline in Siberia–a genetic and simulation-based study. *Biogeosciences*, *16*, 1211–1224. https://doi.org/10.5194/bg-16-1211-2019

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, *90*(1), 68–77. https://doi.org/10.1046/j.0022-0477.2001.00630.x

Kullman, L. (2007). Tree line population monitoring of Pinus sylvestris in the Swedish Scandes, 1973–2005: implications for tree line theory and climate change ecology. *Journal of Ecology*, *95*(1), 41–52. https://doi.org/10.1111/j.1365-2745.2006.01190.x

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

MacDonald, G. M., Edwards, T. W. D., Moser, K. A., Pienitz, R., & Smol, J. P. (1993). Rapid response of treeline vegetation and lakes to past climate warming. *Nature*, *361*, 243–246. https://doi.org/10.1038/361243a0

Maes, S. L., Blondeel, H., Perring, M. P., Depauw, L., Brūmelis, G., Brunet, J., Decocq, G., den Ouden, J., Härdtle, W., Hédl, R., Thilo, H., Heinrichs, S., Jaroszewicz, B., Kirby, K., Kopecky, M., Máliš, F., Wulf, M., & Verheyen, K. (2019). Litter quality, land-use history, and nitrogen deposition effects on topsoil conditions across European temperate deciduous forests. *Forest Ecology and Management*, *433*, 405–418. https://doi.org/10.1016/j.foreco.2018.10.056

Manning, P., de Vries, F. T., Tallowin, J. R. B., Smith, R., Mortimer, S. R., Pilgrim, E. S., Harrison, K. A., Wright, D. G., Quirk, H., Benson, J., Shipley, B., Cornelissen, J. H. C., Kattge, J., Bönisch, G., Wirth, C., & Bardgett, R. D. (2015). Simple measures of climate, soil properties and plant traits predict national-scale grassland soil carbon stocks. *Journal of Applied Ecology*, *52*(5), 1188–1196. https://doi.org/10.1111/1365-2664.12478

Meehl, G. A., Goddard, L., Murphy, J., Stouffer, R. J., Boer, G., Danabasoglu, G., Dixon, K., Giorgetta, M. A., Greene, A. M., Hawkins, E. D., Hegerl, G., Karoly, D., Keenlyside, N., Kimoto, M., Kirtman, B., Navarra, A., Pulwarty, R., Smith, D., Stammer, D., & Stockdale, T. (2009). Decadal prediction: can it be skillful? *Bulletin of the American Meteorological Society*, *90*(10), 1467–1486. https://doi.org/10.1175/2009BAMS2778.1

Midgley, G. F., Hughes, G. O., Thuiller, W., & Rebelo, A. G. (2006). Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity and Distributions*, *12*(5), 555–562. https://doi.org/10.1111/J.1366-9516.2006.00273.X

Miller, J. (2010). Species Distribution Modeling. *Geography Compass*, *4*(6), 490–509. https://doi.org/10.1111/j.1749-8198.2010.00351.x

Moser, B., Kipfer, T., Richter, S., Egli, S., & Wohlgemuth, T. (2015). Drought resistance of Pinus sylvestris seedlings conferred by plastic root architecture rather than ectomycorrhizal colonisation. *Annals of Forest Science*, *72*(3), 303–309. https://doi.org/10.1007/s13595-014-0380-6

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., & Beck, P. S. A. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, *10*, 106–117. https://doi.org/10.1038/s41558-019-0688-1

Niinemets, Ü. (2010). A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research*, *25*(4), 693–714. https://doi.org/10.1007/s11284-010-0712-4

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., & Oksanen, L. (2001). Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, *24*(1), 13–24. https://doi.org/10.1034/j.1600-0587.2001.240103.x

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*(11), 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x

Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761), 20170437. https://doi.org/10.1098/rstb.2017.0437

Ottander, C., Campbell, D., & Öquist, G. (1995). Seasonal changes in photosystem II organisation and pigment composition in Pinus sylvestris. *Planta*, *197*, 176–183. https://doi.org/10.1007/BF00239954

Pearson, R., Phillips, S., Loranty, M., Beck, P., Damoulas, T., Knight, S., & Goetz, S. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*, 673–677. https://doi.org/10.1038/nclimate1858

R Core Team, R. (2013). R: A language and environment for statistical computing. In *R Foundation for Statistical Computing*.

Ramirez, J. I. (2021). Uncovering the different scales in deer–forest interactions. *Ecology and Evolution*, *00*(n/a), 1–8. https://doi.org/https://doi.org/10.1002/ece3.7439

Ramirez, J. I., Jansen, P. A., den Ouden, J., Li, X., Iacobelli, P., Herdoiza, N., & Poorter, L. (2021). Temperate forests respond in a non-linear way to a population gradient of wild deer. *Forestry: An International Journal of Forest Research*, *94*(4), 502–511. https://doi.org/10.1093/forestry/cpaa049

Ramirez, J. I., Jansen, P. A., den Ouden, J., Moktan, L., Herdoiza, N., & Poorter, L. (2021). Above- and below-ground cascading effects of wild ungulates in temperate forests. *Ecosystems*, *24*, 153–167. https://doi.org/10.1007/s10021-020-00509-4

Ramirez, J. I., Poorter, L., Patrick, ·, Jansen, P. A., den Ouden, J., Siewert, M., & Olofsson, J. (2023). Top-down and bottom-up forces explain patch utilization by two deer species and forest recruitment. *Oecologia 2022*, *201*(1), 229–240. https://doi.org/10.1007/s00442-022-05292-8

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*, 168. https://doi.org/10.1038/s43247-022-00498-3

Rees, W. G., Hofgaard, A., Boudreau, S., Cairns, D. M., Harper, K., Mamet, S., Mathisen, I., Swirad, Z., & Tutubalina, O. (2020). Is subarctic forest advance able to keep pace with climate change? *Global Change Biology*, *26*(7), 3965–3977. https://doi.org/10.1111/GCB.15113

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P. B., Bermudez, R., Montgomery, R. A., Rich, R. L., Rice, K. E., Hobbie, S. E., & Stefanski, A. (2022). Even modest climate change may lead to major transitions in boreal forests. *Nature*, *608*, 540–545. https://doi.org/10.1038/s41586-022-05076-3

Richardson, D. M., & Whittaker, R. J. (2010). Conservation biogeography – foundations, concepts and challenges. *Diversity and Distributions*, *16*(3), 313–320. https://doi.org/10.1111/J.1472-4642.2010.00660.X

Rupp, T. S., Chapin, F. S., & Starfield, A. M. (2001). Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in Northwestern Alaska. *Climatic Change*, *48*(2–3), 399–416. https://doi.org/10.1023/A:1010738502596

Schleuning, M., Fründ, J., & García, D. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: An extension of trait-based concepts to plant-animal interactions. *Ecography*, *38*(4), 380–392. https://doi.org/10.1111/ECOG.00983

Sjursen, H., Michelsen, A., & Jonasson, S. (2005). Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems. *Applied Soil Ecology*, *30*(3), 148–161. https://doi.org/10.1016/j.apsoil.2005.02.013

Sullivan, P. F., Ellison, S. B. Z., Mcnown, R. W., Brownlee, A. H., & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, *96*(3), 716–727. https://doi.org/10.1890/14-0626.1

Swedish NFI. (2023). *Swedish National Forest Inventory.* The Department of Forest Resource Management. Swedish University of Agricultural Sciences.

Sweet, S. K., Asmus, A., Rich, M. E., Wingfield, J., Gough, L., & Boelman, N. T. (2015). NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. *Ecological Applications*, *25*(3), 779–790. https://doi.org/10.1890/14-0632.1

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An Overview of CMIP5 and the Experiment Design. *Bulletin of the American Meteorological Society*, *93*(4), 485–498. https://doi.org/10.1175/bams-d-11-00094.1

Wickham, H., & Winston, C. (2016). Package 'ggplot2.' *Create Elegant Data Visualisations Using the Grammar of Graphics*, *2*(1), 1–189.

Wiegand, T., Camarero, J. J., Rüger, N., & Gutiérrez, E. (2006). Abrupt population changes in treeline ecotones along smooth gradients. *Journal of Ecology*, *94*(4), 880–892. https://doi.org/10.1111/j.1365-2745.2006.01135.x

Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., Ciais, P., Sitch, S., Friedlingstein, P., & Arneth, A. (2016). Greening of the Earth and its drivers. *Nature Climate Change*, *6*, 791–795. https://doi.org/10.1038/nclimate3004

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., … Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*(9), 1261–1277. https://doi.org/10.1111/ecog.04960

.