Different dispersal rates and declining climate suitability shape future vegetation compositions across the Arctic: implications for the boreal forest - tundra boundary

Running title: Plant dispersal shapes vegetation change

Authors

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Conflict of interest statement

The authors declare to have no conflicts of interest.

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Abstract

Aim: We investigate how species-specific dispersal abilities might influence future Arctic plant distributions and large-scale dynamics at the boreal forest - tundra boundary until 2100

Location: circumpolar terrestrial Arctic (boreal forest, taiga and tundra)

Taxon: 1550 plant species

Methods:

We developed climate-driven species distribution models (SDM) to predict species-specific emerging climate niches under different climate scenarios. The model was parameterized using occurrence data from the Global Biodiversity Information Facility database (GBIF) and temperature and bioclimatic variables from the CHELSA data set. Dispersal rates were assigned to each species using a trait-based approach and were used to predict future habitat with a distance-based probability over time.

Results:

Plant species are predicted to occupy on average only 12.3% (1.5 – 53.9 95% CI) of their emerging climate niches, with half of the species unable to colonize new habitat by 2100 due to limited dispersal distances. In dispersal limited predictions, migration to higher altitudes played a greater role than northward shifts, and decolonization of cells by species (extirpation) due to decreasing climate suitability changed species composition more than dispersal. Boreal tree species were predicted to expand into the tundra reducing the area without trees.

Main conclusions:

Future plant species distributions and resulting large-scale compositions are affected by species-specific dispersal rates. Even though new suitable niches emerge prominently towards the north, higher altitudes might be more relevant given their accessibility by dispersal over the next century. Although climate niche dynamics could support higher plant species richness across the Arctic, overall richness is expected to decline with climate warming due to dispersal limitations. The colonization of new habitats via dispersal in combination with the decolonization of former habitats due to declining climatic

suitability on species level are predicted to cause large-scale changes in species composition especially at the boundary between the boreal forest and the tundra biome.

1. Introduction

Over the last decades, the temperature in the Arctic has increased two to four times faster compared to the global average, and the speed of warming might even accelerate in the near future (Rantanen et al. 2022). As a result, phenologies and species ranges are changing across the entire Arctic (Parmesan et al. 2006). The northward and upward migration of plant species is a frequently reported response to the changes in the climate niche (Iverson and McKenzie 2013; Stewart et al. 2018; Niskanen et al. 2019; Roland et al. 2019). The advance of the boreal forest into the tundra biome is of particular interest, since it might threaten tundra biodiversity and function (Hofgaard et al. 2012) and might lead to a large-scale biome shift (Beck et al. 2011; Berner and Goetz 2022; Montesano et al. 2024). And although forest expansion and shrubification are expected to cause significant changes to the ecosystem (Mod and Luoto 2016), it remains uncertain how Arctic plant communities as a whole will shift their distribution in the near future, and how these changes might drive large-scale structural transformations across the Arctic.

The boreal forest, also known as the taiga, and the tundra represent two of the most extensive and distinct biomes in the Northern Hemisphere, each characterized by unique biodiversity and ecosystem functions. The boreal forests are dominated by coniferous trees, with spruces, pines and firs in northern North America (Nearctic) and mostly larches in eastern Eurasia (Palearctic) (Herzschuh 2020). In contrast, the treeless tundra is mostly covered by mosses and lichens, dwarf shrubs, and forbs (Zhang et al. 2013), being shaped by extreme cold, permafrost, and short growing season (Shaver 1995). Shrubification of the tundra would reduce the albedo of the landscape, thereby contributing to warming and release of the large carbon storage in the permafrost (Myers-Smith et al. 2011; Bonfils et al. 2012; Loranty and Goetz 2012; Pearson et al. 2013; Plaza et al. 2019). During the last decades an obvious change within the biomes has been driven by the longer growing season with increased plant productivity, leading to a greener Arctic (Phoenix and Bjerke 2016; Lara et al. 2018; Arndt et al. 2019; Tømmervik and Forbes 2020). More recently, this has locally been reversed by frequent summer droughts and wildfires, decreasing plant productivity (Phoenix and Bjerke 2016; Tømmervik and Forbes 2020). For the future, we expect that changes in species composition due to range shifts, both within

and across the biomes, will have even stronger effects on the ecosystems, especially the tundra. Today, large parts of the tundra are already suitable for growth of shrubs and trees, and their potential distribution will cover almost the entire tundra by the end of the century (Zhang et al. 2013). While boreal forests expand at their northern edge, they shrink at their southern edge, being replaced by other biomes, which leads to a biome shift (Beck et al. 2011). However, treeline migration seems relatively slow, significantly lagging behind the climate niche (dispersal lag) (Primack and Miao 1992; Svenning and Sandel 2013; Kruse und Herzschuh 2022), e.g. with thermal velocity exceeding species' dispersal by 2 - 4 km/year according to a past simulation (Zani et al. 2023). After the last glacial maximum, the average dispersal rate of 140 studied European plant species was 1.6 km/year, considerably varying with dispersal mode, as e.g. brown bears (*Ursus arctos*) can transport seeds about 6 km/year. (Cunze et al. 2013). Since the last glaciation, the North American jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) have migrated 19 km and 25 km per century, respectively (Payette et al. 2022). During the 19th and 20th century, the White spruce *(Picea glauca)* treeline moved up to 100 m into the tundra in Alaska (Suarez et al. 1999). For the 21st century, recent models forecast a much faster advance of the treeline, e.g. the individual-based model by Kruse und Herzschuh (2022) predicts a migration of larches of up to 3 km/year under climate warming.

The ability of a plant species to colonize habitats within its climatically suitable niche depends on various factors (McNichol and Russo 2023), but it is primarily constrained by its dispersal capacity (Eriksson 2000; Kruse et al. 2019). Plants can be dispersed by wind (anemochory), water (hydrochory) and animals (zoochory), or the seeds simply fall to the ground, thus the dispersal distance is only about the height of the parent's stem (local non-specific) (Bierzychudek 1982; Hughes et al. 1994; Lososová et al. 2023). Besides these dispersal modes, other plant traits, e.g. the height and growth form, determine the possible dispersal distance of a species (Lososová et al. 2023). Herbs occurring in deciduous forests often do not have special dispersal mechanisms, thus their seeds only disperse locally, and vegetative reproduction is common (Bierzychudek 1982). Short and cold summers hinders sexual reproduction (Bell and Bliss 1980), thus, tundra plants reproduce only infrequently at their northern distributional limit (Molau 1993). Still, most species reproduce via seeds, but can additionally reproduce

vegetatively (Billings 1987) or via vivipary (Molau 1993), resulting in very local dispersal as the next generation evolves close to the parent plant. Considering dispersal constraints in predictions of future climate niches has the potential to provide more realistic scenarios of potential changes in distributions of single species and entire communities.

Species distribution models (SDMs) combine species occurrence data with environmental variables to predict distributions across landscapes, also extrapolating in space and time (Elith and Leathwick 2009). SDMs are based on the assumption that species occurrences are in equilibrium with their climate niche, however this assumption is usually violated when species shift their range under changing climate conditions (Václavík and Meentemeyer 2011). Beside the dispersal lag, which refers to the limited dispersal abilities, there is the establishment lag, which implies that the species are facing difficulties to establish due to e.g. competition with the present community, and the extinction lag, describing the phenomenon that species will stay in their old apparently unsuitable habitats for a longer time than expected as living individuals do not die instantly and seeds are still stored in the soil (Alexander et al. 2018). From these different time lags, a disequilibrium between vegetation and climate results, which is difficult to predict (Svenning and Sandel 2013) but is still important to be included in models forecasting spatio-temporal changes (Alexander et al. 2018). Nevertheless, most species distribution models do not account for these lags. Implementation of these constraining mechanisms is possible in models that are based on cellular automates (Engler et al. 2012; Zani et al. 2023), but difficult to tackle in statistical (correlative) models. Probably as pioneers, Shipley et al. (2022) implemented dispersal in a statistical SDM, calculating the probability of dispersal based on supplied dispersal rates using exponential distributions, while Jaeschke et al. (2013) had cut their predictions of Odonata range shifts using ArcGIS.

In this study, we applied statistical SDMs implementing species-specific dispersal rates based on plant trait information, and conducted an additional analysis regarding the extinction lag. Our goal was to investigate how the different dispersal abilities of species might impact the large-scale dynamics at the boreal forest - tundra boundary large-scale until 2100. We hypothesized that constraining dispersal

rates lead to smaller distribution changes compared to the potential of emerging habitats. However, even though there are relatively small changes within species, the consequent changes in species composition may still cause structural changes across the Arctic. Considering a large-scale approach, we separately modeled the distribution of 1550 terrestrial plant species, to predict (1) emerging suitable climate niches across the Arctic, (2) the area that can potentially be colonized by plant species given the dispersal constraints, and (3) spatial patterns of range shifts with a focus on northward movements. By combining the future prediction of all species ranges, we test the hypothesis that (4) changes on species level can lead to large-scale changes at the boundary between the boreal forest and the tundra biome until 2100.

2. Material and Methods

2.1 General modeling approach

We applied climate-driven species distribution models (SDM) to predict emerging niches for plant species across the Arctic boreal forest, taiga and tundra. Based on trait specific dispersal distances, we compared emerging areas with the areas that could effectively be reached and potentially be colonized given species-specific dispersal capacities. Covering the entire terrestrial Arctic with a 25 km x 25 km resolution, our model predictions aim to generate insights into landscape-scale dynamics of species distributions, how large-scale patterns may change due to ongoing climate change, and how species-specific dispersal affects predictions. All analyses were performed using R Statistical Software (version 4.3.1; R Core Team 2023) and a release of the model code will be published on Zenodo after acceptance). For more details see the ODMAP protocol (Appendix S1) according to the criteria by Zurell et al. (2020) and further information in the Appendix S2, S3 and S4 in Supporting Information.

2.2 Selecting species occurrence data, background data and environmental predictor variables

To define the current climate niches of plant species occurring in the circumpolar Arctic (defined by the boreal forest/taiga and tundra polygons according to Olson et al. (2001) all available presence data was retrieved from the Global Biodiversity Information Facility using the package ‘rgbif’ (v.3.7.8) (GBIF.org, GBIF Occurrence Download on 26 March 2024). Occurrence data was filtered and cleaned following standard protocols (GBIF Secretariat 2021). Missing values in longitude, latitude and species as well as error values were discarded and fossil records/museum specimens were excluded. We selected for the time after 1970 and a distance uncertainty < 5000 m. This data is registered with GBIF as a derived dataset (doi:10.15468/dd.y4uq5q) and is available on Zenodo (https://zenodo.org/records/16925866). We performed grid-based thinning by retaining one occurrence per cell of the 5 km x 5 km environmental grid (see below). Given the circum-arctic scale, sampling biases are strong and skewed towards Europe (Figure 1a). Spatial filtering is commonly applied to reduce sampling bias (Veloz 2009; Kramer-Schadt et al. 2013). Therefore, we additionally applied spatial filtering on the observations after the grid-based thinning in order to maximize equal spatial representation by generating random sample points within a 150 km distance and then selected the closest occurrence point to each of these points.

Finally, only species with at least 175 total occurrences were used to set up the model. The filtered occurrence data was split into test (25%) and training (75%) data, with at least 150 training data points per species.

Background data was generated using a similar approach as described in Senay et al. (2013) by specifying the geographical extent for sampling with a buffer around presence points and environmental profiling of the background using a one-class support vector machine classifier.

As predictors variables for the environmental conditions, we used the CHELSA V.2.1 Climate dataset (Karger et al. 2017; Karger et al. 2021) with 30 arc seconds spatial resolution that was upsampled to a resolution of 5 km x 5 km (equal-area projection) (downloaded on 27th March 2024). For the model calibration, historical monthly weather data for 1981 – 2010 was utilized. For the future projections, future climate data calculated by the global climate model GFDL-ESM4 CMIP6 I was downloaded. GFDL-ESM4 was chosen because when only using one of the best five models, this one should be prioritized according to the technical specification of the CHELSA data (CHELSA 2021) which follows the prioritization of the Intersectoral Impact Model Intercomparison Project (ISIMIP)3b (ISIMIP 2021). The ISIMIP is an international network of climate-impact modelers that provides a framework for consistently projecting the impacts of climate change across affected sectors and spatial scales (Schellnhuber et al. 2013). As predictor variables we chose bioclimatic variables, representing seasonal and annual statistics of temperature and precipitation (cf. Hijmans et al 2005). We included bio1 (annual mean temperature) and bio12 (annual precipitation) as basic variables for each species, and added all others of the 19 bioclim variables that remained after collinearity removal. For the overall importance of the parameters, see Appendix S2, Figure S2.1, and for the predictor variables for each species, see Appendix S3. The data was given as monthly means for 30-year periods, which we averaged to annual means. We used the data for the periods 2011 – 2040, 2041 – 2070 and 2071 – 2100 (hereafter, referred to as 2040, 2070 and 2100) for the scenarios ssp126, ssp370 and ssp585. These integrated scenarios couple the Representative Concentration Pathways (RCP) that describe the additional radiative forcing of 2.6, 7.0 and 8.5 W/m^2 (IPCC, 2014), with the shared socioeconomic pathways (ssp).

Ssp1 is the path shifting to a more sustainable future, ssp3 is characterized by regional rivalry and international fragmentation and ssp5 is marked by a fossil-fueled development with population growth in high income countries and population decreases in developing countries (O'Neill et al. 2017).

2.3 Predicting future niche suitabilities with species distribution models

To predict future niche suitabilities, we used the MaxEnt model (Phillips et al. 2006), implemented in R package 'dismo' (v. 1.3.14). MaxEnt is considered to have high predictive accuracy (Merow et al. 2013) even with presence-only data, using background data instead of (pseudo-)absences (Phillips et al. 2006). We predict the climate suitability (0 - 1) of the present time slice (1981 – 2010) for all 1550 plant species based on the thinned occurrence points, the generated background data and the climate data (for settings see Appendix S2). To transfer the continuous output (0 - 1) into binary values (0 or 1) we used the MaxEnt prevalence threshold "10 percentile training presence" which describes that 90% of all input occurrence points are included in the probabilities above the threshold (for values see Appendix S3).

2.4 Implementation of dispersal constraint

Dispersal was implemented by considering species-specific dispersal rates. For each species, the traits growth form, height, habitat and dispersal-related diaspore features were collected from various databases, literature and websites (see published dataset Farkas et al. (2025) on Zenodo: https://doi.org/10.5281/zenodo.15771333). Based on these traits, the dispersal mode (e.g. anemochory, zoochory) and the resulting dispersal distance class (1 - 6) were assigned to each species according to Lososová et al. (2023) (confer this publication for more detailed information) (Figure 1b). The dispersal distance classes describe the maximum dispersal distance of 99% of the seeds ranging from 1 m (class 1) to 1,500 m (class 6). For each future scenario, based on distance to the closest occurrence (always in relation to the binary map of the presence time slice) and a sigmoidal probability function parameterized with the 50% and 99% dispersal distances, the MaxEnt suitability for each cell was set to zero if a random number between 1 and 0 was above the sigmoidal probability value (and original value was kept for random numbers below). For comparison, we also ran a scenario without

the implementation of the species-specific dispersal rates. For this “unconstrained” scenario, we used a normal distribution probability function with mean=1,500 km and sd=250 km.

2.5 Analyzing the advance of the boreal forest and species composition dissimilarity

To study the large-scale dynamics resembling those of boreal forest and tundra, we first selected all tree species that are not reported in literature to also occur as shrub or in prostrate or dwarf forms (see species list in Appendix S8). Then for each cell the ratio between the number of these boreal species and the total number of species was calculated. For one analysis, this ratio was additionally converted to binary (no trees, > 0 % trees) which could be regarded as the simplified equivalents “tundra” and “boreal forest/taiga”, and the latter cells were assigned “Nearctic” or “Palearctic” according to the WWF Terrestrial Ecoregions of the World (Olson et al. 2001) based on their geographic location. The agreement with the established ecoregions was 89% for the “Nearctic boreal forest/taiga” and 93% for the “Palearctic boreal forest/taiga” (see Appendix S7, Figure S7.1). The “no trees” area covered only 63% of the “tundra” ecoregion, which is caused by our implementation that the predicted presence of one tree species typical for the boreal in a cell turns it to a “boreal forest” cell, which is a simplification as the tundra is characterized by typical species. For better readability, in the following we use “tundra” for our “no tree” area (but keep in mind the real tundra area is larger) and “boreal forest” for the biome “boreal forest/taiga”, but still mean the conglomerate. When interpreting the results, it has to be taken into account that in reality, changes of the ecoregions can differ as the agreement of the different areas in our study with these ecoregions is not 100%. To analyze the change in species composition, we stacked all species distribution maps and calculated the Jaccard dissimilarity index to show the dissimilarity of the species composition of 2040, 2070 and 2100 compared to 2010, ranging between 0 “total similarity” and 1 “total dissimilarity”. In addition to the constrained and unconstrained scenarios, we added a “no extirpation” scenario, meaning that species may only colonize new cells but may not disappear if the climate niche becomes unsuitable.

2.6 Credible intervals and significance testing

Slopes were estimated with linear regression using the function ‘lm’ from ‘stats’. We then simulated

1000 values from the joint posterior distribution of the parameters of our linear model using the function ‘sim’ from the package ‘arm’ (v.1.14.4) and used the 2.5% - 97.5% quantile as upper/lower limit of the 95% credible intervals. Significant differences were tested with the Wilcoxon test using the function ‘wilcox.test’ from the package ‘stats’ (v. 4.3.1).

3. Results

Averaged over the SDMs for all 1550 species the AUC was 0.89 ± 0.07 for training data and 0.87 ± 0.09 for test data. The Boyce Index (ranging from -1 to 1) was 0.81 ± 0.15 for training data and 0.69 ± 0.26 for test data.

3.1 Reachable share of emerging habitats

The new suitable habitat area that could emerge with climate warming tended to increase over time and under more extreme climate scenarios (Figure 2a). By 2100, according to the climate scenario ssp585, each species was predicted to gain 4 * 10^6 km² (median) of new suitable habitat within the studied area of approximately 24 * 10^6 km² (ssp126: 3.9; ssp370: 4.1). However, 844 species (54%) could not colonize new habitats at all. The remaining species could only reach 12.3% (median) (1.5 – 53.9 95% CI) of their new habitat areas by dispersal, when averaged over all time slices and scenarios (ssp126: 9.3%, 12.4, 18.1; ssp370: 9.6, 11.6, 14.9; ssp585: 9.4, 11.2, 14.3).

In our model, we restricted dispersal by assigning six distinct dispersal distance classes to the species based on their traits. Based on the classification, the majority of the species (57%) was limited to dispersal distances of less than 150 m/year. This classification significantly influenced the extent of new area species could colonize, ranging from 0% for the shortest dispersal distance (class 1) to 36% (mean) for the longest distance (class 6) of the emerging habitat area for the respective species (Figure 3a). Means are given in the following as medians are 0 for several groups. The dispersal mode (e.g. as anemochory, zoochory) is the most important determinant of a species' dispersal distance class, following the classification by Lososová et al. (2023). Our analysis indicated that species classified as local dispersers (1 - 5 m) were not predicted to colonize any new habitats by 2100. Species dispersed by myrmecochory (which belongs to class 3) could barely colonize new habitats either, as they could only reach 2.5 * 10^{-5}% of the new emerging niche (Figure 3b). In contrast, species dispersed by anemochory could reach 8.7%. Species dispersed by zoochory and hydrochory, with dispersal distances of up to 1500 m/year, could colonize a much larger share (33.2% and 39.3%) of their emerging habitats.

Growth form also plays a role in defining colonization potential and thereby the dispersal distance class. Aquatic species, predominantly classified under mode “Hydrochory” and dispersal class 6, were predicted to reach 37.6% of the new habitats (Figure 3c). Among terrestrial plants, shrubs showed the highest colonization potential (19.7%), followed by trees (15.9%), ferns (9.4%) and bryophytes (8.5%). Forbs (5.4%) and graminoids (4.3%) were predicted to colonize the smallest share of their emerging habitats. Species belonging to growth forms typical for the boreal forest thus tend to have a larger colonization potential than tundra species.

3.2 Spatial patterns of new habitats

Our analysis revealed distinct spatial patterns in the emergence of new habitats under a warming climate. The model predicted a northward shift of emerging habitats over time for the unconstrained scenario (ssp126: slope (absolute values) 1.76 km/year, 1.73 – 1.79 95% CI; ssp370: 3.18, 3.16 – 3.19 95% CI; ssp585: 3.03, 3.01 – 3.04 95% CI) (Figure 2b). The habitats that could be reached under dispersal limitation showed a northward shift as well (ssp126: 2.16 km/year, 2.10 – 2.22 95% CI; ssp370: 1.53, 1.48 – 1.58 95% CI; ssp585 1.49, 1.44 – 1.54 95% CI). The climate scenarios did not exhibit a linear impact on the shift.

Species richness showed a general decrease towards the north, with a species hotspot in Scandinavia and the lowest richness in Greenland (Figure 4a). The maximum cell species richness was predicted to decline from 1251 in 2010 to 1006 (constrained) and 1202 (unconstrained) by 2100 (Figure 4b, c). The mean number of species per cell was projected to decrease from the current 437 (median 403) to 326 (median 328) in the constrained scenario and increase to 505 (median 526) in the unconstrained scenario by 2100 for climate scenario ssp585 (Figure 4f).

Colonization patterns were strongly influenced by dispersal abilities. Most colonizations (Figure 4d, e) occurred near areas of current high species richness (Figure 4a). The maximum number of new colonizing species per cell was 130 in the constrained scenario and 578 in the unconstrained scenario (Figure 4d, e). Altitude also played a role in colonization patterns, with most colonizations occurring around 1200 m in the constrained scenario and around 0 and 1400 m in the unconstrained scenario

(Figure 4g).

3.3 Large-scale vegetation changes

The advance of the boreal forest area was more pronounced for the unconstrained (Figure 5b) than for the constrained scenario (Figure 5a). The "Palearctic boreal forest" was predicted to colonize more new cells until 2100 than the "Nearctic boreal forest" (Figure 5d, right), while the latter showed a significantly (Wilcoxon test: $p < 2.2e-16$) larger shift of the new cells to the north (Figure 5d, left). Both the northward shift and the increase in “boreal forest” cells as well as the decrease of the “tundra” (no trees) cells was much more pronounced for the unconstrained scenario compared to the constrained scenario. While the slow dispersers (species belonging to dispersal distance class 1 – 3) dominated almost all cells in 2010, until 2100, is was predicted that more than 50 % of the species will be quick dispersers (species belonging to dispersal distance class 4 – 6) in most cells of our study region in the constrained scenario.

The species composition showed increasing dissimilarity compared to 2010 over the time slices (Figure 6). For the unconstrained scenario (Figure 6b) dissimilarity was higher and increased faster than for the constrained scenario (Figure 6a). To distinguish between the effects of new colonizations and climate-driven decolonizations, we included an additional scenario based on the constrained scenario assuming no extirpation, i.e. species could not decolonize cells in which they occurred in 2010. In this scenario, the dissimilarity stayed very low over all time slices (Figure 6c). Hence, the decolonization of cells by species (extirpation) due to decreasing climate suitability seems to be a significant factor driving the species composition, being more important than dispersal under constrained conditions.

4. Discussion

We investigated how the different dispersal abilities of species might impact the species composition and the large-scale dynamics of the boreal forest - tundra boundary until 2100 by predicting species-specific emerging climate niches under different climate scenarios. Our results overall confirmed our hypothesis that dispersal rates might strongly influence future species distributions as only a small part of emerging climate niches is reachable, yet potentially triggering a shift of the boreal forest - tundra boundary.

4.1 Limitations and validation

Our study focuses on the effects of dispersal constraints on the climate change-induced changes in species distribution. However, biotic interactions can influence the rate and direction of range shifts in plants as well (HilleRisLambers et al. 2013). Competition may slow range shifts at lower limits but facilitation may accelerate upward range shifts of arctic plants. (Ettinger and HilleRisLambers 2017). As competition can truncate a species' fundamental niche and confine its poleward range boundary, competitive native tundra vegetation could limit the expansion of tall shrubs into the Arctic tundra (Angers-Blondin et al. 2018; Armitage and Jones 2020). Thus, beside dispersal lag, establishment lags may delay colonization rates as a result of, e.g., competition (Alexander et al. 2018). Still, strong competitive abilities of tall deciduous shrubs mainly control shrub expansion in the Arctic (Mekonnen et al. 2021), thereby reducing the persistence of competitors in the native plant community due to increased competition (Usinowicz and Levine 2021). Extirpation lags may delay the disappearance of species from their established habitats because of long-living individuals (having resources in storage organs) and ongoing recruitment from soil seed banks (Alexander et al. 2018) (aka extirpation debt, e.g., Tilman et al. 1994). Due to the lack of empirical data for parameterization, we only included the dispersal lag, and focused most analyses on the new colonized cells to investigate the colonization potential.

For most of our analyses, we included both new colonizations and decolonizations, ignoring the impact of establishment and extirpation lag. We assumed a counterbalancing effect based on observations by

Rumpf et al. (2019a), who found equal shift rates for the leading edge (establishment) and rearing edges (extirpation) of species, leading to a stable range size. However, the duration of establishment lags can differ between species (e.g. Robeck et al. 2024), and not all species show an extirpation lag (Rumpf et al. 2019b). We did not consider the rearing edge of the “boreal forest” invaded by species originating from outside the study area. Comparing our results to a no-extirpation assumption (Figure 5c) led to less pronounced changes, clarifying that decolonizations due to declining climatic suitability can substantially impact species composition, and hence extirpation lag could have a large effect. Regarding environmental parameters, we focused on large-scale changes and did not include non-climatic factors such as site fertility, which are important on a local scale (e.g., Schibalski et al. 2014).

Despite the coarse resolution and lack of non-climatic parameters, our model delivered results that overall agreed with observations and expected trends reported in literature. The dispersal distances we assigned following Lososová et al. (2023) seemed to be appropriate estimates when compared to dispersal rates from literature for various species (see Appendix S5, Table S5.1). The present distribution we modeled is similar as reported in literature, e.g. for *Picea glauca* in Alaska (Ohse et al. 2009) (see Appendix S6, Figure S6.1). The future predictions of our model agree with observations like those of Kullman (2008) who observed a northwards and upwards shift of thermophilic species such as *Alnus glutinosa* in Scandinavia. The overall pattern of decreasing species richness towards the north, with a richness hotspot in Scandinavia and the least species in Greenland, aligns with literature as well (Mutke and Barthlott 2005; Pironon et al. 2020). Aiming for a validation in the field, during an expedition to Ulukhaktok (Northwestern Territories, Canada) in summer 2025, 43 different plant species were identified in the field, out of which 31 species were also included in this study. Comparing these presences to the model result for the present time slice (1980 – 2010), 71 % were predicted correctly. Comparing the 2025 field records with the model prediction for 2010 – 2040 shows an agreement of 84 %, while 16 % of the recorded species were predicted as absent. Given the low spatial coverage of GBIF occurrence points in the Northwestern Territories (Figure 1a), 84 % agreement in a random location can be regarded as a solid result, supporting the accurateness of the model.

4.2 Multiple responses to warming on species level

Species range shifts to the north were not predicted as pronounced as expected. We found a northward shift in the predicted emerging habitats (as reported by Stewart et al. 2018; Roland et al. 2019), but considering different dispersal abilities, only a small share or even nothing of the predicted new habitat area could be reached. Consequently, dispersal abilities significantly impact the future of individual species by defining their capacity to follow their climate niche under changing climate conditions. However, even trees, which belong to the faster dispersers, will probably not be able to keep up with the predicted shift of their climate niche until 2100 (Hanberry 2024).

Besides the northward shift, another response of species to increasing temperatures is the colonization of higher altitudes (MacDougall et al. 2021). In our model prediction, we also observed that under dispersal limitation the peak of colonizations occurred at higher altitudes than under unconstrained conditions, where a colonization peak occurred at 0 m. This suggests that suitable climate niches at higher altitudes may serve as more relevant refugia due to higher accessibility, while those at higher latitudes remain largely unreachable. In response to warming, particularly non-boreal species migrate to higher elevations, thereby also responding to boreal taxa that tend to expand their distribution ranges (MacDougall et al. 2021).

Dispersal abilities could substantially determine to which extent richness decline can be counterbalanced, as species richness was even predicted to increase on average without dispersal limitation while it decreased when considering dispersal. New colonizations can only occur within the dispersal distance of a species around occurrence points. Each presence cell of a species might generate seeds for colonization of nearby areas and might function as a source patch according to the metacommunity concept, which describes metacommunities as a combination of source and sink patches (Marquet and Velasco-Hernández, 1996; Leibold et al. 2004). Dispersal to sink habitats can be advantageous under changing environmental conditions as sources can become sinks and vice versa (Holt 1997). Initially, new colonized habitats might act as sink patches for populations due to suboptimal soil or nutrient conditions or because beneficial biotic interactions are not established yet.

According to the concept of meta-ecosystems, sink patches could get enriched with nutrients from other patches which can facilitate the establishment of populations (Gravel et al. 2010). When populations become fully established, these patches could transform into source patches potentially functioning as stepping stones for species migrating to higher latitudes and altitudes.

The compositional changes we observed were not only caused by species migrating northwards, but even more resulted from species disappearing locally as suitable habitats were predicted to decline with climate change in southern areas. This demonstrates the potential significance of considering extirpation lag to improve model predictions. In reality, a decline in the southern distributions of specialist species of the tundra might additionally occur because these species are less competitive and thus might be outcompeted by generalist species which expand their areas northwards (Callaghan et al. 2004; Callaghan et al. 2005; Pykälä 2017).

4.3 Large scale vegetation changes

The varying responses to climate warming on species level suggest that there might be different responses on the large scale as well. In our study we predict an increase in "boreal forest" area, while the "tundra" area decreased. Hence, cells that belonged to the “tundra” in 2010 shifted to “boreal forest” cells. This process is based on a single mechanism in our model: Fast dispersing tree species migrate northwards and colonize new habitats, thus potentially invading an area without trees and turning it into “boreal forest”. Additionally, our model also showed that species decolonize cells in their old habitats as habitat suitability declines due to climate warming, which also changes the species composition that characterizes tundra or boreal forest regions. The species of the “tundra” region had overall smaller dispersal rates compared to the boreal species. Thereby, the "tundra" region could lose species that decline due to increasing climate stress while boreal species immigrate from the south.

Thinking beyond the scope of our model, it could be hypothesized that native tundra plants could successfully integrate into the invading "boreal forest" if they have similar ecological functions as the species that dropped out. This hypothesis is supported by observations of species being replaced by closely related species from the same genus (Schmidt et al. 2012). In contrast, competition of the

immigrated boreal forest species can put additional stress on the native tundra species, accelerating their decline (Callaghan et al. 2004). Competitive exclusion by invaded species might even more likely make tundra species become extinct than temperature increase (Pykälä 2017). Consequently, boundary regions could change their biome affiliation over time as their vegetation composition increasingly resembles that of the boreal forest, resulting in a shrinking tundra area.

Spatial configuration complicates the general trend of northward shifts, as there are no more northern land masses in regions like Siberia (Pearson et al. 2013). The tundra's proximity to the sea in most of its original region may restrict northward expansion. Our model predicted that the "Nearctic boreal forest" will migrate further than the "Palearctic boreal forest". The Nearctic landmass extends further north than the Palearctic landmass, resulting in a larger suitable area emerging at the same longitude as temperatures increase. Palearctic species could colonize more cells than Nearctic species as the Palearctic landmass is larger than the Nearctic landmass, so for the same temperature increase, a larger area becomes suitable at the same latitude. Thus, beside dispersal constraints, geographic constraints may impact the range shifts of large-scale vegetation assemblages.

4.4 Further implications

The predicted patterns of vegetation change can be expected to occur delayed and less pronounced in reality, as we included neither the extirpation lag nor the establishment lag. Parts of the changes we observed are based on predicted species extirpations due to declining climatic suitability. Under the assumption of no extirpations the changes in species composition were predicted to be less pronounced. Moreover, successful colonization depends not only on dispersal abilities but is also impacted by e.g. competition that can lead to an establishment lag.

For future studies, we recommend incorporating dispersal constraints, which were shown to substantially impact species distributions. Additionally, extirpation and establishment lag times, or, in case of mechanistic models, species interactions and species-specific time until maturity that can cause these time lags, should be included as these factors also impact the realized niche of species. To predict changes of the entire ecosystem, integrating animals would be necessary, as herbivory could

counteract the predicted dynamics of the vegetation.

As climatic stress and competition of invasive species but also other factors like land use change and pollution are threatening biodiversity in the Arctic (Ksenofontov et al. 2018), innovative conservation measures are crucial. For instance, the protection of climate refugia, areas that remain relatively stable despite broader environmental change, is important, as these refugia offer vulnerable species the chance to persist and potentially re-expand (Keppel et al. 2012). Moreover, a proactive strategy to protect threatened species is assisted migration (aka assisted colonization, managed translocation), the deliberate relocation of species to areas where they are more likely to survive under future climate conditions (Hällfors et al. 2014). Although this approach is controversially discussed, it might be reasonable to bring the seeds of poor dispersing tundra species further north, where plants are barely established today, as the tundra is threatened to lose area at its southern edge which becomes invaded by boreal forest species. However, careful consideration of ecological impacts and ethical implications is essential when implementing such interventions (cf. Hunter 2007; Richardson et al. 2009; Minteer and Collins 2010; Aubin et al. 2011; Hewitt et al. 2011; Sáenz-Romero 2021).

4.5 Conclusion

Comparing a dispersal unconstrained scenario with a scenario considering species-specific dispersal rates, we found that different dispersal abilities can impact future species distributions, determining their abilities to follow the predicted climate niche shift. Even though new habitats emerge prominently in higher latitudes, higher altitudes might be more relevant as refugia due to better accessibility by dispersal. Although climate niche dynamics could support higher plant species richness across the Arctic, overall richness is expected to decline with climate warming due to dispersal limitations. The colonization of new habitats via dispersal in combination with the decolonization of former habitats due to declining climatic suitability are predicted to cause substantial changes in species composition, also leading to large-scale changes at the boundary between the boreal forest and the tundra biome.

Figures with captions

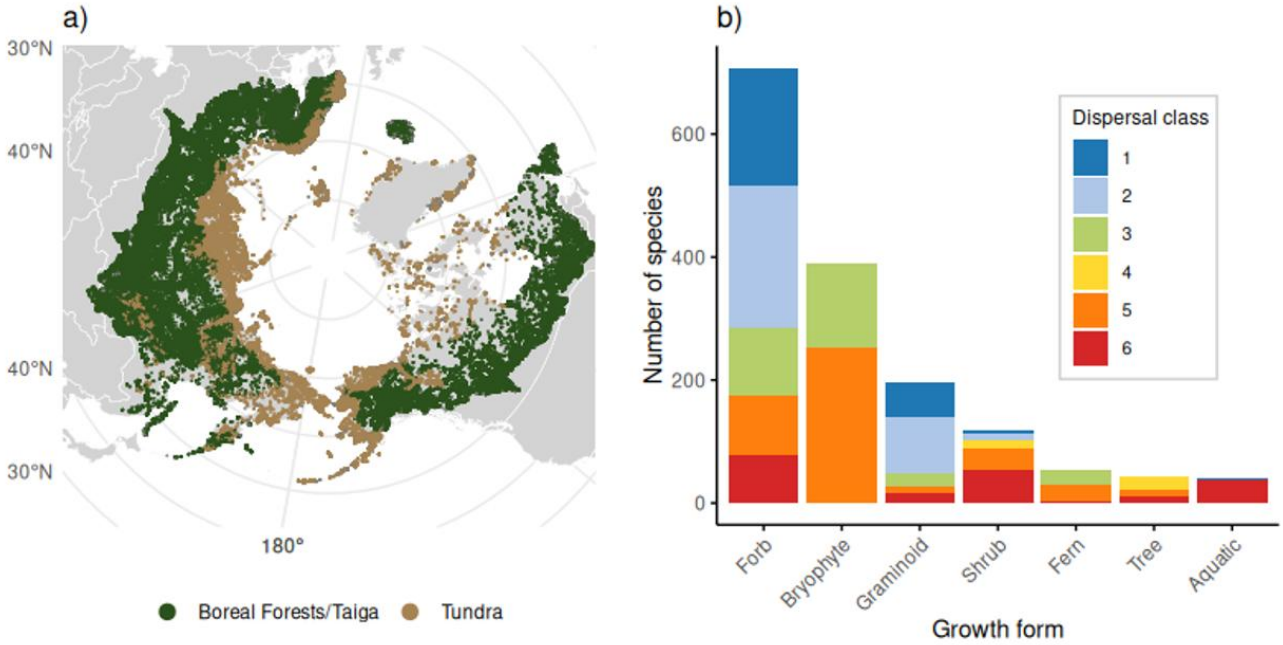


Figure 1: *(a) Spatial distribution of downloaded and spatially thinned Plantae records from GBIF (Global Biodiversity Information Facility) database for the boreal forest/taiga and tundra (defined following Olson et al. 2001). Map is presented in the Lambert Azimuthal Equal Area projection. Green observations belong to the boreal forest/taiga, and brown observations to the tundra biome. (b) Six different dispersal classes and seven growth forms were assigned to the Plantae species. The dispersal distance classes were assigned according to Lososová et al. (2023) and describe the maximum dispersal distance of 99% of the seeds ranging from 1 m (class 1) to 1,500 m (class 6). These distances were the basis for the dispersal constrained predictions.*

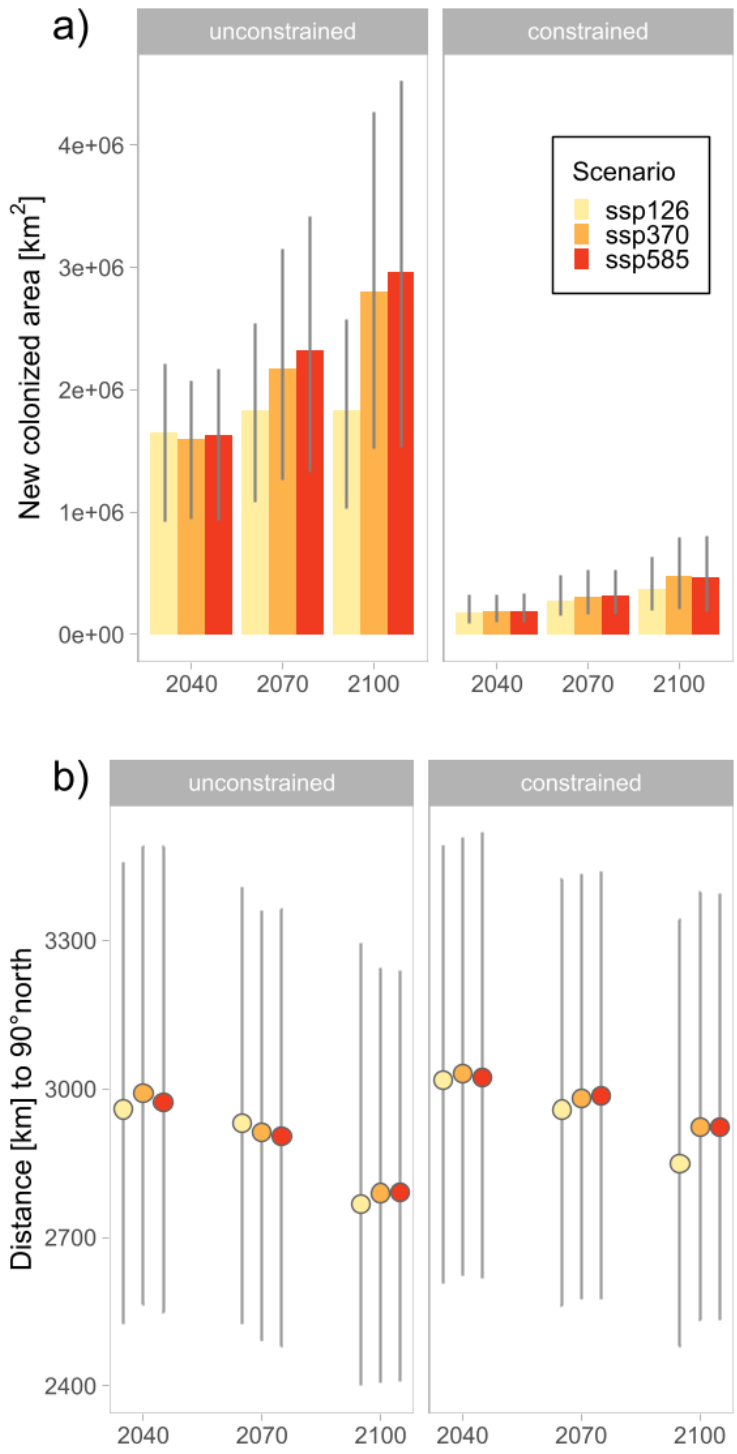


Figure 2: *(a) New colonized area [km^2] for the unconstrained and species-specific dispersal constrained scenario (compared to 2010) averaged over all studied 1550 arctic plant species. (b) Distance [km] to 90° north of new suitable cells (unconstrained) and newly colonized cells (dispersal constrained) (delta to time slice before) averaged over all 1550 species. New cells are defined as cells which indicated "absence" in 2010 and turned to "presence" in the respective future time slice. The circles with error-bars show the median and the 25% and 75% quantiles. All data is shown for the three future time slices and the three climate scenarios (ssp126, ssp370, ssp585) visualized by the colors.*

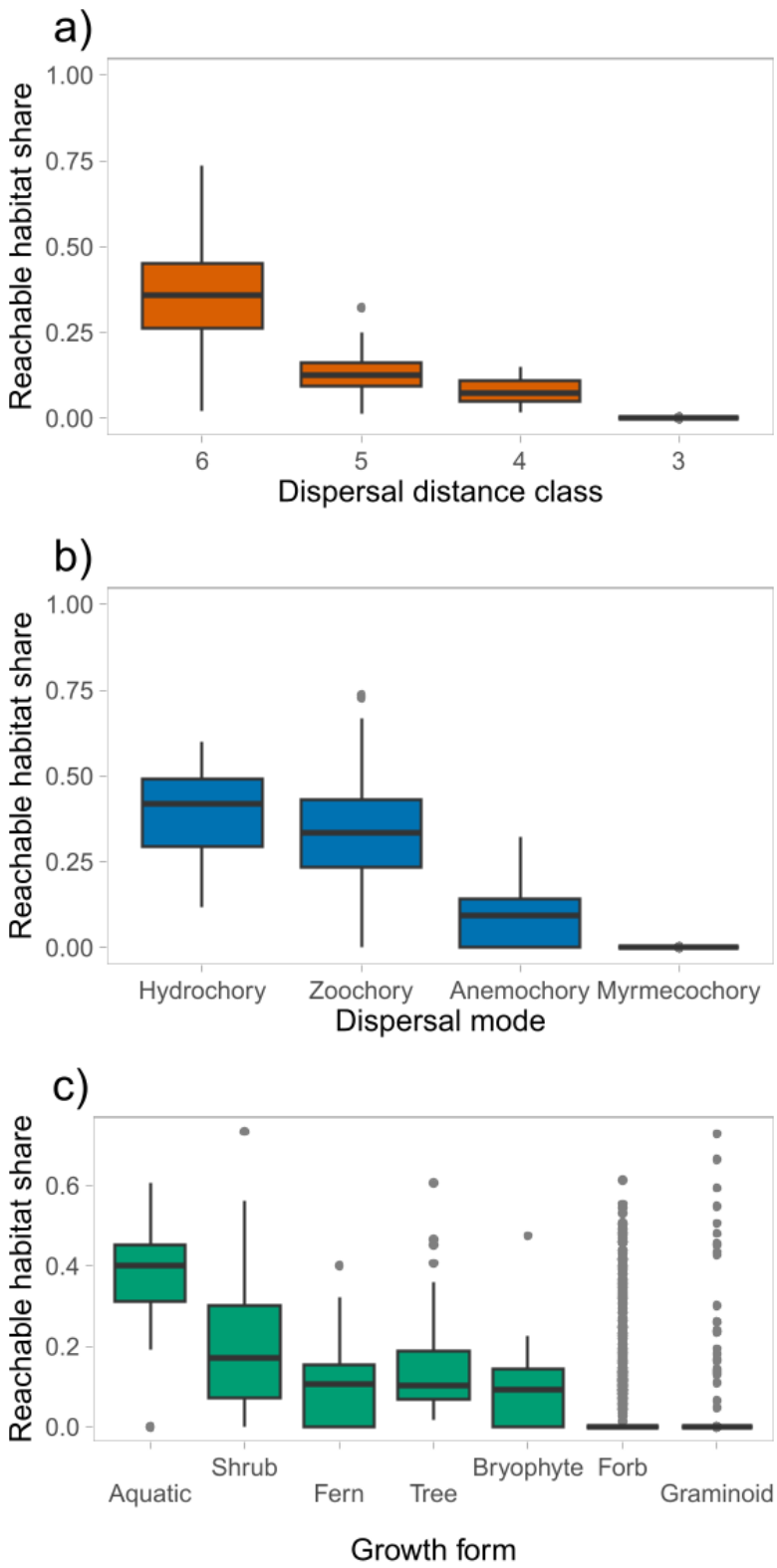


Figure 3: *Reachable habitat share, i.e. new colonized cells in 2100 (climate scenario ssp585) compared to 2010 for the dispersal constrained scenario divided by the new colonized cells in 2100 (climate scenario ssp585) compared to 2010 for the unconstrained scenario for the (a) dispersal distance class, (b) dispersal mode and (c) growth form.*

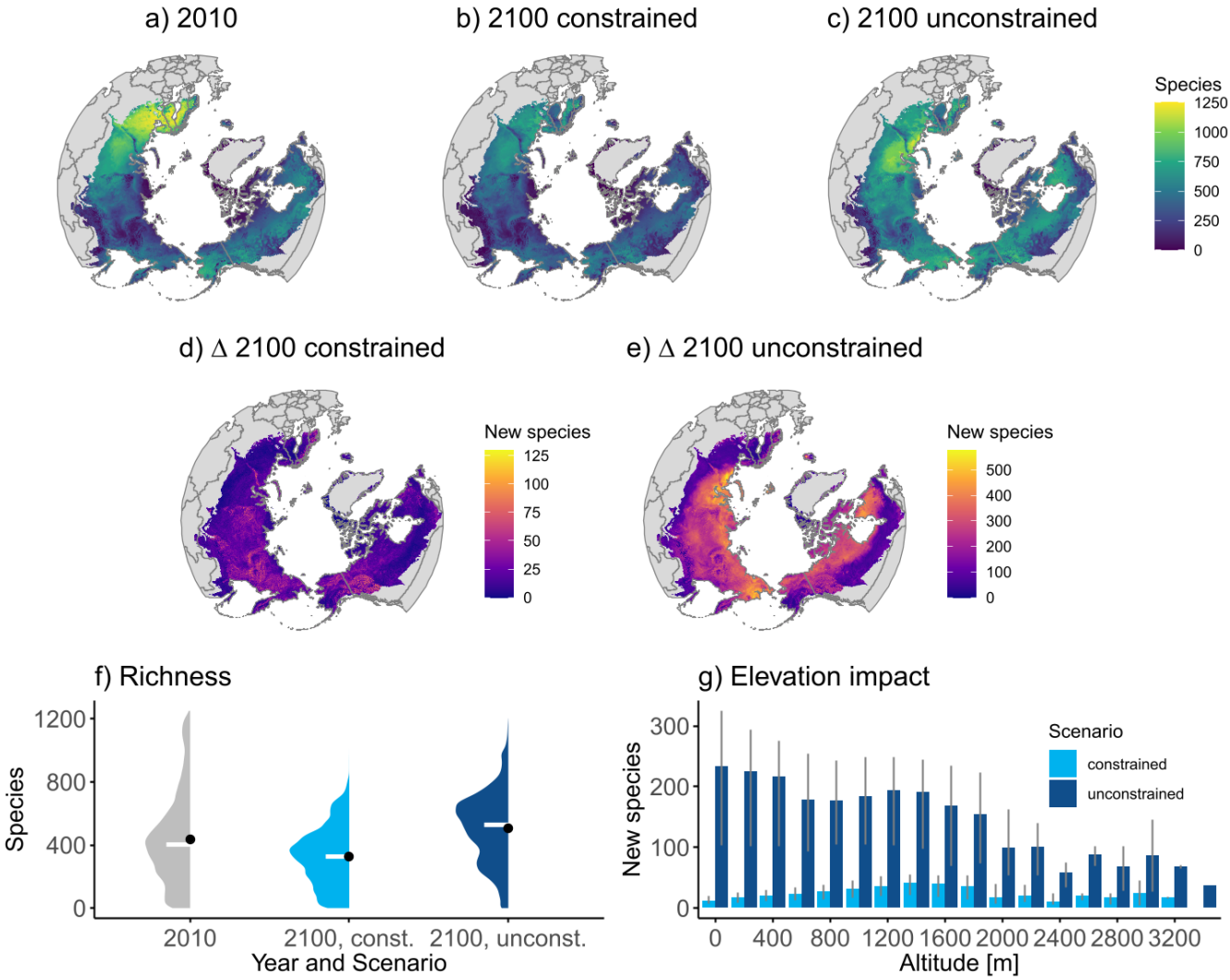
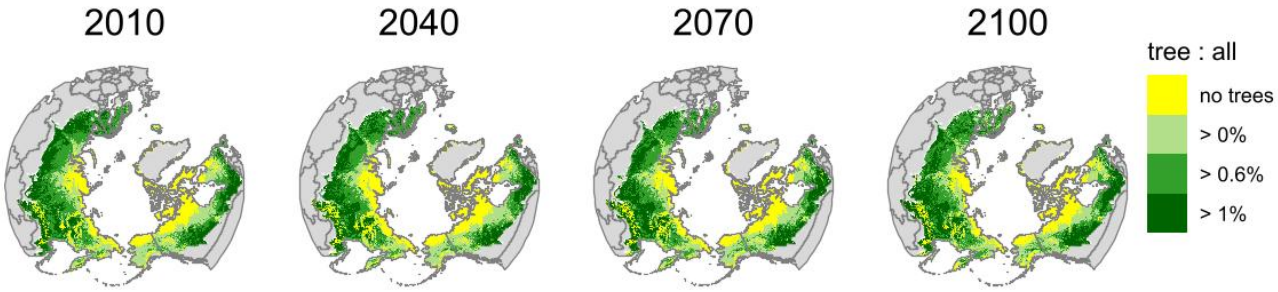
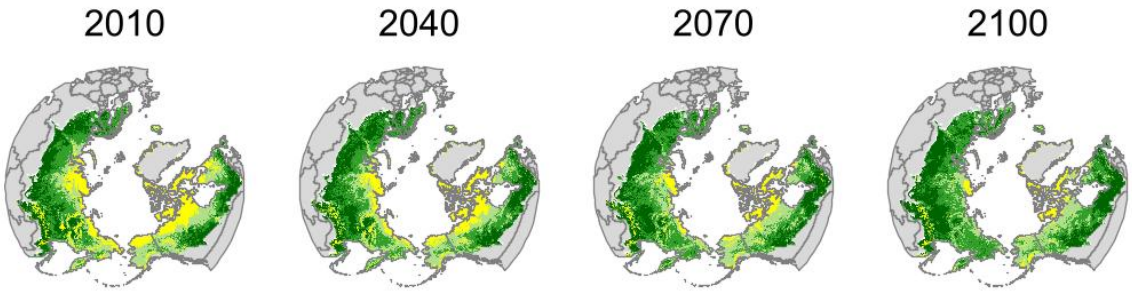


Figure 4: *Number of all studied 1550 arctic plant species per cell for (a) present and for 2100 (last of three time slices) for climate scenario ssp585 (maximum scenario out of three) for the (b) species-specific dispersal constrained and (c) unconstrained scenario. Number of only new colonizing species by 2100 (climate scenario ssp585) compared to 2010 for the (d) dispersal constrained and (e) unconstrained scenario. The plots show the sum of the distribution maps of all 1550 species (a - c) and the difference of the sum between 2100 and 2010 (d - e). All maps are presented in the Lambert Azimuthal Equal Area projection. (f) Number of all species per cell as half violin plot for the data shown in (a), (b) and (c). (g) shows the number of new species over different altitudes for the constrained and unconstrained scenario. The grey error bars show the 25% and 75% quantiles.*

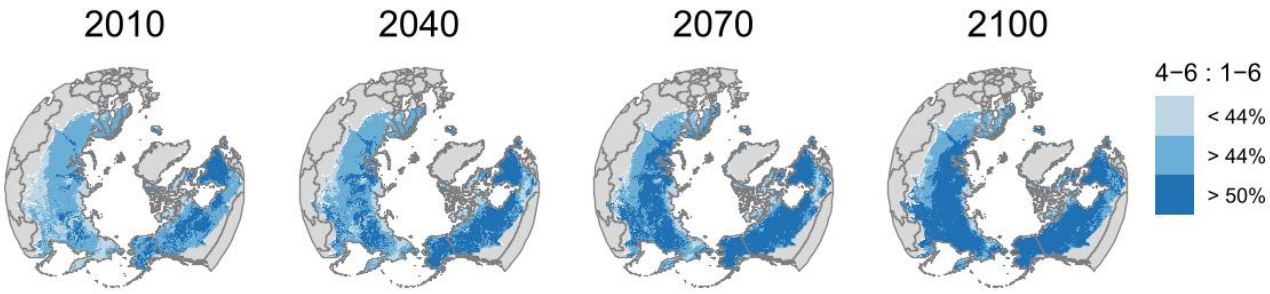
a) Share of tree species in total species per cell (constrained)



b) Share of tree species in total species per cell (unconstrained)



c) Quick dispersers (classes 4−6) vs. all dispersers (classes 1−6)



d) Nearctic vs. Palearctic boreal forest: northward shift and cell colonization

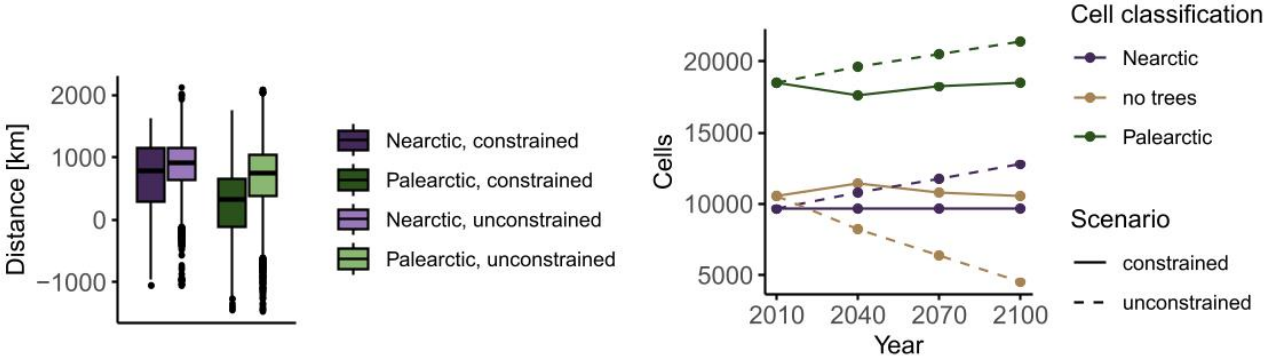


Figure 5*: Shift of boreal forest - tundra boundary over time (2010, 2040, 2070, 2100) for climate scenario ssp585 (maximum of three scenarios) visualized as share of tree species in total number of species per cell for (a) dispersal constrained scenario and (b) unconstrained scenario.(d) Northwards shift of the boreal forest regions in Nearctic and Palearctic from 2010 to 2100 for constrained and unconstrained scenario (left) and number of cells over time for the dispersal constrained scenario (solid line) and unconstrained scenario (dashed line). The cell conglomerates were named according to their geographic position in the realms and the similarity to the biomes of the boreal forests (incl. taiga) and the Arctic tundra ("no trees" (Olson et al. 2001), were the presence of at least one tree species defines the "boreal forest" hence the underlying data is the binary version of the ratio shown in (a) and (b).*

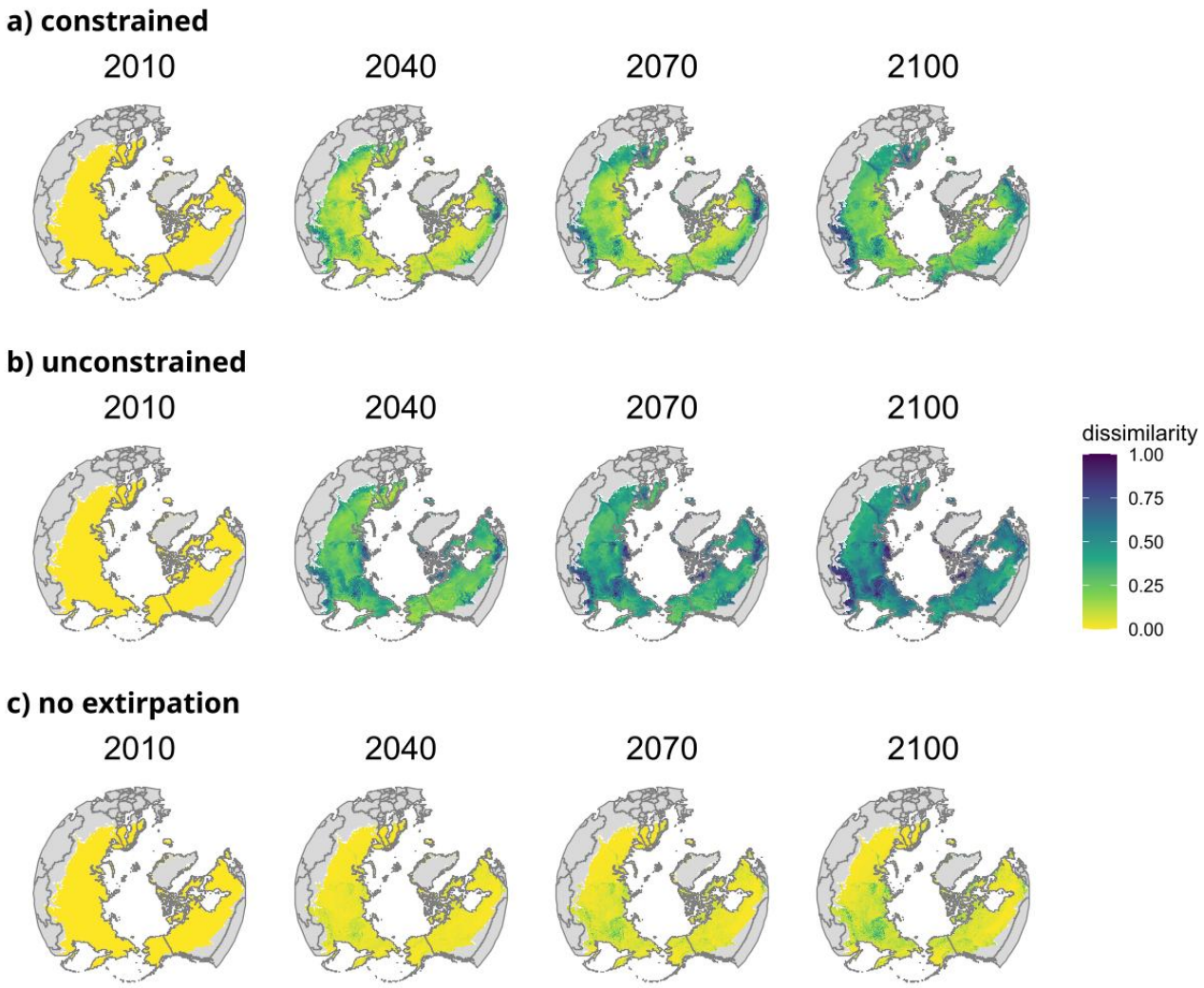


Figure 6: *Impact of dispersal vs. extirpation: Dissimilarity (Jaccard index) of species composition compared to 2010 over time for (a) constrained, (b) unconstrained and (c) no extirpation scenario (based on constrained scenario). Here, no extirpation means that species may only colonize new cells but may not disappear if the climate niche becomes unsuitable (see discussion for potential reasons and implications).* The Jaccard dissimilarity index ranges between 0 “total similarity” and 1 “total dissimilarity”. *[double column]*

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