Plant traits poorly predict winner and loser shrub species in a warming tundra biome

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Data archiving statement

Code and data will be made available at the time of publication in an open-access repository (GitHub) and have a DOI number assigned through Zenodo.

Abstract

Climate change is leading to a species redistributions. In the tundra biome, many shrub species are expanding into new areas, a process known as shrubification. However, not all tundra shrub species will benefit from warming. Winner and loser species (those projected to expand and contract their ranges, and/or those that have increased or decreased in cover over time), and the characteristics that may determine success or failure, have not been fully identified. Here, we investigate whether current range sizes are related to plant trait values and intraspecific trait variation by combining 17,921 trait records and distribution data from 62 shrub species across three continents (>30 degrees north). In addition, we determine which traits are associated with species projected by species distribution models to expand or contract their ranges under climate change, and species that have undergone past cover changes over time. Winner and loser shrub species identified from projected range shifts generally differed from those identified from observed past cover change. We found that greater variation in seed mass and specific leaf area were related to larger projected range shifts. Projected winner species generally had greater seed mass values than 'no change' and loser species. However, contrary to our expectations, traits' values and variation were not consistently related to current and projected ranges, and depended upon the future climate scenarios considered in range projections. There were no clear relationships either between cover change over time and trait values or variation. Overall, our findings indicate that abundance changes and projected range shifts will not lead to directional modifications in shrub trait composition or variation with future warming, since winner and loser species share relatively similar trait spaces based on commonly measured traits. Future research could investigate other morpho-physiological traits underpinning climatic preferences, which might better predict future range and abundance changes.

Keywords

Climate change, traits, global change ecology, intraspecific trait variation, range dynamics, species abundances, species distributions, tundra biome.

Introduction

The Arctic is warming at three to four times the rate of the global average (Chylek et al., 2022; Rantanen et al., 2022), resulting in reported shifts in biodiversity and changes in ecological processes. In particular, the phenomenon of ‘shrubification’ has been extensively described across the tundra biome (García Criado et al., 2020; Martin et al., 2017; Myers-Smith, Forbes, et al., 2011; Naito & Cairns, 2011; Sturm, Racine, et al., 2001; Tape et al., 2006), with shrub species experiencing faster growth and reproduction, increases in height (Forbes et al., 2010; Macias-Fauria et al., 2012) and expanding into new areas (Myers-Smith, Forbes, et al., 2011; Pellissier et al., 2010; Sturm, Racine, et al., 2001). These processes may cause reshuffling of species compositions and functional diversity, thus affecting ecosystem function for the tundra region and surrounding vegetation through biotic interactions (Alexander et al., 2015; Mod et al., 2016; Niittynen et al., 2020). Despite shrubs’ dominance increase over other functional groups, both increasing and decreasing shrub cover have been reported at certain sites (Hollister et al., 2005; Maliniemi et al., 2018), and we do not yet know whether expanding and contracting shrub species share similar traits.

Shifts in traits at the community level have already been observed, with taller species spreading in a warming Arctic (Bjorkman, Myers-Smith, et al., 2018). However, the biome-level relationships between trait values and intraspecific variation for a given species and its geographic distribution have yet to be quantified for tundra shrub species. These biome-scale relationships could dictate why some shrub species are expanding/increasing (winners) and others are contracting/decreasing (losers), and whether some species are not changing. Different methods to monitor species exist, but in this study we compare two different scales: past changes in cover over time in monitoring plots, and biome-scale projections of species ranges using species distribution models (SDMs); two metrics that are generally positively related as per the abundance-range size theory (Gaston & Blackburn, 2008).

The pattern of species moving polewards and towards higher elevations by tracking warming temperatures has been discussed for over two decades (Chen et al., 2011; Hastings et al., 2020; Hickling et al., 2006; Parmesan et al., 1999). Tundra species distributions are the result of long-term glacial history and inherent Arctic geography. Palaeoecological evidence indicates shrub expansion into the Arctic during the warmer Last Interglacial and the Holocene post-glacial period (Birks, 2008; Crump et al., 2021; Higuera et al., 2008), signalling that rising temperatures are likely to result in further shrub expansion across the tundra (Gałka et al., 2018). Current range shifts are mediated by processes derived by climate change including permafrost thaw and extended season length (Sturm, Holmgren, et al., 2001), and factors like snow cover, nutrient availability and species interactions, but also by the amount of potential habitat and species' colonization capabilities. These, in turn, are determined by reproduction, dispersal and establishment success – which could favour generalist species with greater dispersal ability, reproductive rate, and competitive ability to expand into new areas (Alsos et al., 2007; Angert et al., 2011; Venn et al., 2021). For instance, dwarf birch (*Betula nana*) and tall willow (*Salix* sp.) species are expanding across the tundra due to their flexible colonization strategy featuring clonal growth and high seed dispersal capacity, respectively (Andruko et al., 2020; Formica et al., 2014; Myers-Smith, Hik, et al., 2011; Ropars & Boudreau, 2012). Thus, certain traits could most likely influence whether tundra species will expand or contract under climate change.

Plant traits have been widely used to assess species relationships with their environment (Violle et al., 2007). As traits vary across environmental gradients, they can be indicators of plant responses to climatic conditions (Díaz et al., 2016; Shipley et al., 2016; Soudzilovskaia et al., 2013) and represent relevant dimensions of functional and strategic variation between plant species (Pollock et al., 2012), at both species and community levels (Bruelheide et al., 2018). Plant traits are linked not only to environmental responses but also to ecosystem functions like carbon storage and nutrient cycling (Aubin et al., 2016; Lavorel & Garnier, 2002). Typically, trait-based analyses use a single mean trait value per species at the global level (Violle et al., 2007), disregarding individual variability information (Betway, Hollister, May, Harris, et al., 2021; Bolnick et al., 2011; Myers-Smith, Thomas, et al., 2019; Siefert et al., 2015; Thomas et al., 2019, 2020). Trait variation between and within populations can be markedly different (Lamy et al., 2011), and is ultimately driven by differences among individuals, rather than between species (Siefert et al., 2015). Thus, intraspecific trait variation (ITV) might have a stronger influence on ecological dynamics than previously thought (Bolnick et al., 2011; Jessen et al., 2020). However, ITV has not been extensively accounted for in trait-based ecology (Moran et al., 2016), despite accounting for 25% of total trait variation within communities, 32% among communities (Siefert et al., 2015), and 23% of trait variation in tundra biome-wide data (Thomas et al., 2020).

Traits that are related to dispersal, colonisation and growth can provide insights into which species are more likely to expand or contract their ranges as the climate changes. A trait framework that represents major axes of plant life history variation is the leaf-height-seed strategy scheme defined by Westoby (1998), which describes a plant’s strategy based on its specific leaf area (SLA), plant height and seed mass. Plant height relates to competitive ability, with tall plants shading out shorter competitors. SLA is linked to carbon investment per area of light capture, and plants with greater SLA obtain nutrients more easily. Seed mass is related to dispersal and colonisation abilities because lighter seeds generally travel further, though larger seeds tend to have higher germination success and seedling survival (Hamilton et al., 2005). In the tundra, resource economics traits occupy much of the global trait space, while structural traits such as plant height are relatively more restricted (Thomas et al., 2020; Wright et al., 2004). Nevertheless, shrub species still show large relative variability, reaching maximum heights of up to 3-4m among the species included in this study. Since traits can explain species’ responses to biotic and abiotic factors and influence their competitive ability (Aubin et al., 2016; Lavorel & Garnier, 2002), we would also expect traits to influence how species’ distributions change in a warming climate.

Species Distribution Models (SDMs) have arisen as a flexible tool to quantify current species ranges and project their potential range shifts by combining species occurrences with geospatial information on current and future climate variation (Guisan & Thuiller, 2005; Thuiller et al., 2019). However, SDMs have been criticised for their failure to incorporate evolutionary history, biotic interactions, or realistic dispersal. Thus, range projections cannot fully reflect future species distributions in the same way as collected range change data over time (Dormann, 2007; Pearson & Dawson, 2003). Moreover, SDMs are correlative methods where the outcomes are based on statistical relationships among variables and an assumption that species are currently in equilibrium. Nonetheless, SDMs still provide useful estimates of potential future suitable habitat in the absence of observational data (Elith & Leathwick, 2009), and some SDMs now incorporate dispersal ability and additional parameters such as morpho-physiological traits and their phenotypic plasticity to improve projections, thus making more realistic future predictions (Chardon et al., 2020; Cunze et al., 2013; Fordham et al., 2012; Garzón et al., 2019; Normand et al., 2013; Pollock et al., 2012). If the processes of survival, reproduction, dispersal and colonisation determine a plant's range, then range shifts should be associated with species' traits related to these processes. In the warming tundra biome, community composition (Elmendorf et al., 2012; Myers-Smith, Forbes, et al., 2011; M. D. Walker et al., 2006) and certain size-related and resource economics traits are changing across time and space (Bjorkman, Myers-Smith, et al., 2018; Thomas et al., 2020). However, the relationships between species' traits and their current range size or potential for range shifts have not been explored.

In this study, we combine species trait, range and abundance data to understand whether median trait values (MTV) and intraspecific trait variation (ITV) are associated with current range sizes in tundra shrubs. Additionally, we determine which categorical and continuous traits are associated with species projected to expand or decrease their ranges, and that have increased or decreased in abundance over time. Considering the magnitude of observed vegetation changes in tundra ecosystems, plant traits could be a particularly relevant tool to understand range dynamics across a warming Arctic. Here, we address the following questions:

1) *Can traits explain current shrub species range sizes?*

Greater height and SLA are linked to competitive ability and resource acquisition (Díaz et al., 2016), and small-seeded species are associated with longer dispersal and greater seed production (Hamilton et al., 2005). Thus, we expect taller shrubs with greater SLA values and lower seed mass to have the largest current range sizes. We hypothesise that ITV in all three traits is positively related to species' range sizes, since they could reflect greater adaptations to environmental variability. Greater genetic or phenotypic variation could provide more scope for natural selection and adaptation (Bolnick et al., 2011) and thus potentially increase species' chances of adapting to diverse and fluctuating environmental conditions (Kumordzi et al., 2019).

2) *Do traits correspond with projected shrub range shifts and past cover change?*

Tundra plant species occurring in warmer climates tend to have greater height and SLA (Betway, Hollister, May, & Oberbauer, 2021; Bjorkman, Myers-Smith, et al., 2018), and warmer conditions are expected to expand in the near future (Pearson et al., 2013). Thus, we expect that individuals occupying warmer climatic niches and having more competitive strategies (greater height and SLA values) and increased dispersal capacity (small seeds) will occupy larger projected ranges and have undergone cover increases under a warming climate. We also hypothesise that species with greater ITV in all three traits will have greater projected ranges as they are likely to be adapted to a wider climatic niche in their current range, and thus undergo future range expansion with warming.

3) *Which are the winner and loser shrub species in a warming tundra and what are their trait combinations?*

Tall plants with wind-dispersed seeds are usually more competitive as they have facilitated seed dispersal and shade shorter plants (Westoby, 1998). We expect winners (those projected to expand their ranges or having increased in cover) to be mainly tall shrubs, given that they are the current dominant life form in warmer niches, and losers (those projected to contract their ranges) to be mostly dwarf shrubs, which tend to predominate in the colder part of the climatic niche (D. A. Walker et al., 2005). We hypothesise that species with greater ITV in all traits will be winners, and vice versa for losers. Finally, we presume that species that have increased in cover are also projected to experience range expansions with warming, following the abundance-range size relationship theory (Gaston & Blackburn, 2008).

Methods

Definitions and taxonomy

The tundra is defined as the region beyond the elevational and latitudinal treeline (Berdanier, 2010). We consider shrubs as multi-stemmed woody plants under 5-6 m in height (Wilson, 1995). We followed the taxonomy outlined in The Plant List (http://www.theplantlist.org/) at the species level and standardised synonyms according to this reference. Definitions of the three traits follow Kattge et al., (2020) which in turn follow Garnier et al., (2017).

Trait data

We extracted a total of 17,921 trait records from the TRY 5.0 (Kattge et al., 2020) and the Tundra Trait Team (TTT) databases (Bjorkman, Myers-Smith, et al., 2018) for three plant size and economics traits related to competitive ability and dispersal (plant height, SLA and seed mass) for 62 shrub species across three continents (**Figure 1, Table S4-S6**). From the total, three trait records were from the literature and 192 records were collected by the authors and unpublished thus far. We removed the observations with values greater than four standard deviations from each species mean following the protocol outlined in Bjorkman et al. (2018). Functional traits have been correlated to each other in the literature (Dupré & Ehrlén, 2002; Moles & Westoby, 2004; Pollock et al., 2012), but we did not find correlations between the traits in this dataset that might have influenced our statistical outcomes (**Table S2.17-19**).

We retained all georeferenced records above 30 degrees north in latitude, as we were interested in trait variation per species beyond tundra biome values. Trait data from more southern latitudes could be indicative of the trait changes that tundra species could experience in a warmer future due to adaptation, phenotypic plasticity or gene flow (Bjorkman et al. 2018, Thomas et al. 2020). We included non-georeferenced trait records from databases that we were certain contained records from high-latitude ecosystems (e.g., if an approximate location/site name was provided). We retained only records that reported single values and individual means. We kept control and ambient values only and removed all experimental treatments and herbarium specimens as we were interested in traits from unmanipulated wild specimens. For each species-by-trait combination, we only retained those with more than four records, providing a dataset with 62 species. We calculated ‘trait values’ (MTV) as the median per species and ‘trait variation’ (ITV) as the standard deviation (SD) of all trait values per species (**Figure 1**). We chose SD as a commonly used ITV metric with a more conservative data distribution than others like the coefficient of variation (COV); however both metrics were directly proportional (**Table S4-S6, Figure S6**). We compared ITV values using a random sample of five records versus all available records and found very similar data distributions, thus we opted for including all available records for ITV calculation (**Table S4-S6**). We log-transformed the median and SD values with the natural logarithm because the differences between species are better characterised on a log-scale (Bjorkman, Myers-Smith, et al., 2018; Thomas et al., 2020; Westoby, 1998).

To explore the influence of categorical traits, we obtained data on taxonomic family, functional group, dispersal mode and deciduousness from a variety of sources including TRY and online florae combined with expert knowledge (see ‘Online sources of categorical traits and maximum height’ in Appendix). To group species according to height, we extracted the potential maximum canopy height per species from online florae (see Appendix) and assigned the species a category following the classification in Myers-Smith et al. (2015): dwarf shrubs (< 20 cm), low shrubs (20 - 50 cm), and tall shrubs (> 50 cm). Maximum canopy height is a relevant method to classify species given our interest in the height that species could achieve in warming conditions (i.e., current height of species at sites outside the Arctic), rather than its average representative height in the Arctic. We used values from online florae rather than TRY/TTT values to avoid circularity in defining functional groups. This could mean that online florae values (mostly from the Arctic) would reflect shorter values than TRY/TTT (which include records outside the Arctic).

When screening identified duplicate records per species, trait, coordinates and collector/databases, we consulted the original datasets (when available) to investigate if potential duplicates were actual values. If both values (i.e., including duplicates) appeared in the original dataset, they were considered valid records. We removed records that were clearly duplicates (*n* = 129), either because they were found both in TRY and TTT, or because the original database showed no duplicates. We identified two mistakes in trait units or coordinates, which we double-checked with the original data contributors and corrected accordingly.

Since we only had original seed mass data for 28 species (as opposed to 57 species for SLA and 52 species for height), we gap-filled seed mass data for an additional 12 species that had data on both height and SLA but no seed mass data. To gap-fill, we extracted data at the genus level above 60 degrees north (to ensure Arctic representative records) and for which there were records for over four individuals. We then calculated the log-transformed median value and the SD at the genus level and included these 12 values for the gap-filled species (**Table S1**).

To account for confidence depending on the number of observations, we calculated an index value per species-by-trait combination. Species with over 20 observations were assigned an index value of 1 and gap-filled species or those with five observations had an index value of 0.5. For species with between 6 and 19 observations, we calculated the index following a linear regression (see below), where N_{obs} is the number of observations per species-by-trait combination:

$$Index = 0.33 + \left(\frac{1}{30}\right) * \mathrm{N}_{\mathrm{obs}}$$

We used this index to down-weight species with smaller numbers of records in the weighted regressions explained below (Christensen 2019, Bürkner 2017). We also calculated a combined index per species by averaging the individual trait indices together.

Range size data

We used projected current range sizes to represent present-day species ranges (see Appendix). To characterize projected shifts in species range size (hereafter ‘range shifts’), we used SDM-derived distribution data for 62 species under 24 future climatic scenarios as calculated by Blach-Overgaard et al. in prep (see ‘Species distribution modelling’ in Appendix for details). Blach-Overgaard et al. calculated a ‘no dispersal’, a ‘limited dispersal’ and an ‘unlimited dispersal’ scenarios. A ‘limited dispersal’ accounts for species-specific future migration rates, which were calculated using species-specific dispersal capacities in a linear mixed models framework following Tamme et al. (2014), and estimate how far a species can disperse using dispersal-related traits including plant height and seed size in order to quantify more ecologically relevant range shifts. A ‘limited dispersal’ scenario incorporates geographical constraints, while an ‘unlimited dispersal’ climatic scenario (without dispersal rates) means that species in one continent could spread to another, e.g., North American species would have available ranges in Europe, and vice versa. Thus, ‘unlimited dispersal’ scenarios do not consider geographical realities and would likely over-estimate range sizes. We compared the three dispersal scenarios and concluded that a ‘limited dispersal’ scenario would be the most realistic and thus chose this scenario as representative of range shifts (**Figure S1**). We also determined that the potential circularity on using the ‘limited dispersal’ scenario does not influence the main findings of this study (see ‘Use of traits in model projections’ in Appendix, **Figure 5, Figure S2**, **Table S2**).

Projected species range shifts were computed both as relative (%) and absolute (km^2), and ‘range shifts’ only reflect a change in the overall range size over time (not changes in the shape or location of the ranges). We refer to ‘range shifts’ when we include both projected increases and decreases in total range size, and to ‘range expansions’ and ‘range contractions’ when referring to projected range size increases and decreases, respectively (**Figure 1**). We log-transformed (with the natural logarithm) and centred current range sizes as the values were not always normally distributed and included outliers. Since the projected range shift data included negative values, we first divided the absolute range changes by a million km^2 and the relative range changes by 100, in order to bring the values closer to zero. We then added a constant value (the negative minimum value plus one) so all values were positive, and afterwards log-transformed these values. Finally, we centred these values on zero before carrying out the statistical analysis in order to facilitate convergence (Harrison et al., 2018, Bolker et al. 2013).

Classification of winner and loser shrub species

We classified winner and loser shrub species using 1) projected range shifts from the SDMs (into the years 2070 – 2099) and 2) cover change over time from the International Tundra Experiment (ITEX) dataset (between 1970 - 2010). For range shift projections, we calculated the 25%, 50% and 75% quantiles of species’ projected range shifts across the 24 climatic scenarios (both for absolute and relative range shifts) and categorised species as winners (if the 25% quantile was above zero), no change (if any quantile overlapped zero) or losers (if the 75% quantile was below zero). For cover change over time, we analysed shrub cover change over time from 105 subsites and 30 sites from the ITEX network (Henry and Molau 1997). Based on the analysis by Bjorkman et al. (2018), individual species’ relative cover change over time per plot were modelled as ordinal numbers using a Poisson distribution with subsite and site as random effects, aggregating after to subsite and species level. Thus, we obtained slopes of cover change per year for each species-by-site combination. We defined winner, no change and loser cover categories according to whether these slopes per species across all sites were positive or negative, and whether the 95% credible intervals overlapped zero (**Figure S3, Table S3**).

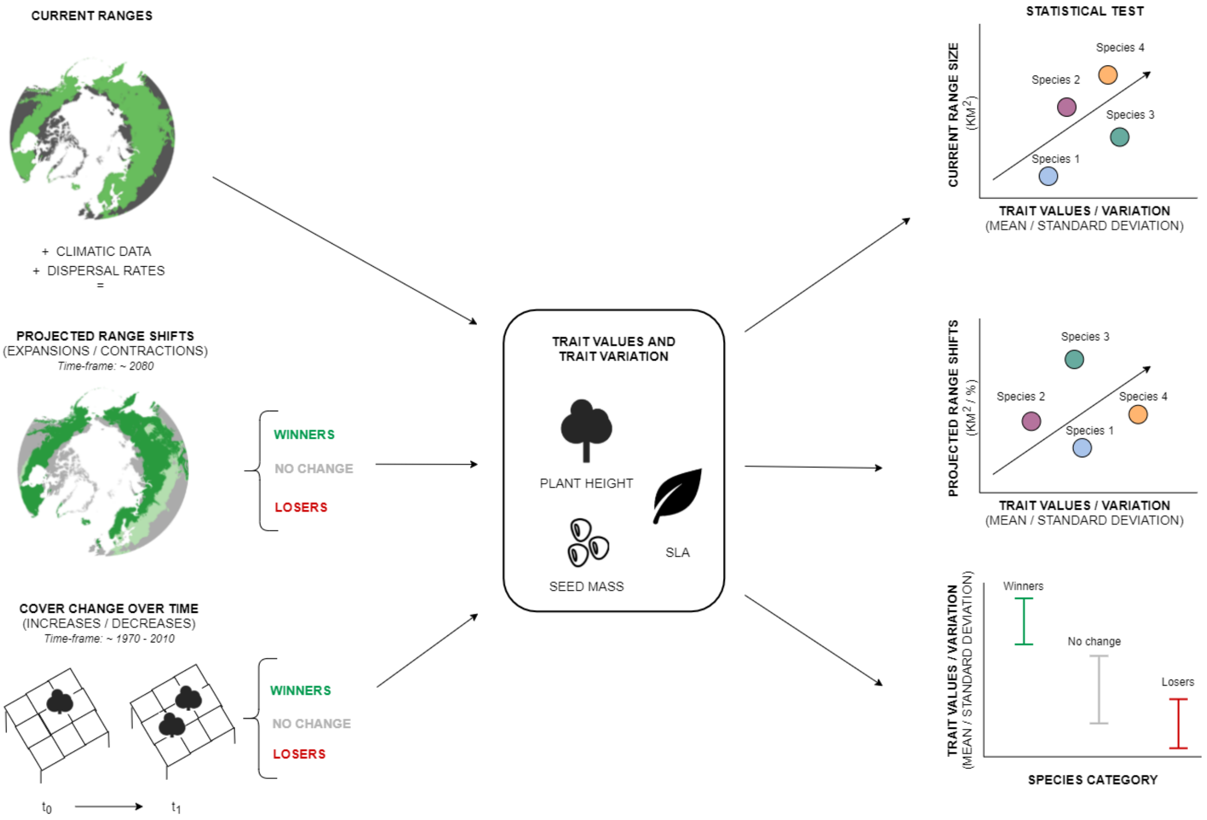

Figure 1. Conceptual diagram of the different types of data used in this study and their relationships. In the current range map, green represents the current distribution of a species. In the projected range shifts map, different green shades in the map represent the difference between current and projected ranges. In the cover change over time drawing, the point-framing grid represents cover change over time. Categories of winner, no change or loser species were identified following two different methods: based on future projections of range shifts, and based on past cover change over time. Current range sizes were modelled with trait values and variation, and projected range shifts (which could be range expansions or contractions) were modelled as a function

of trait values and variation. Cover change over time species categories were modelled with trait values and variation.

Statistical models: Current range sizes and traits

To understand whether species' ranges were associated with traits, we fitted weighted linear regressions per trait of species' current range sizes as a function of MTV, weighting each record according to the scoring index described above. We also modelled current range size as a function of the three traits' MTV together for those species which had trait data for all three traits (weighting according to the combined index), and as a function of three two-way interactions of these three traits. To evaluate whether range size was explained by categorical traits, we fitted separate models with current range size as a function of deciduousness (evergreen/deciduous), functional group (tall/low/dwarf shrub), dispersal mode (berry/wind-dispersed) and taxonomic family. We modelled MTV as a function of species' range category (winner, no change, loser) per trait to identify differences in trait values between the different species categories. We also modelled categories as a function of all three different traits to understand whether winners differed in their trait combinations from loser and no change species (as this was indicated in the PCA analysis described below). To do this, we fitted an additive weighted binomial model with a Bernoulli distribution by assigning a value of 0 to loser and no change species, and a value of 1 to winners. We do not include here the variant of that model with an interaction element since the model did not converge with that level of complexity. Finally, we fitted similar weighted regressions as described above, with the same structure but with ITV instead of MTV (**Figure 1, Table S2**).

Statistical models: Species range shifts and traits

To understand if species' range shifts were associated with traits, we fitted weighted linear regressions of relative and absolute range change as a function of MTV per trait, each with the 25%, 50% and 75% quantile range change (of the 24 climatic scenarios) as a response variable. We also modelled both median relative and absolute range shifts as a function of all three traits (using the combined weighting index), and as a function of their three two-way interactions. To evaluate whether range shifts were explained by categorical traits, we fitted separate models for absolute and relative range shifts as a function of deciduousness, functional group, dispersal mode and family. To understand the processes of range expansion and contraction individually, we fitted separate weighted regressions for species that are predicted to experience range 'gains' and 'losses' (defined as those species whose median range change was above and below zero, respectively, both for absolute and relative changes). We modelled median range 'gains' and 'losses' as a function of trait values per individual trait, and then as a full model with all three different traits, and their three two-way interactions, for absolute and relative changes. We fitted similar weighted regressions as described above, with the same structure but with ITV instead of MTV (**Figure 1, Table S2**). Finally, to understand if traits were related to past cover change, we fitted weighted linear regressions of the slopes of cover change over time (1970 – 2010) as a function of MTV and ITV, and modelled the slopes of cover change over time as a function of all three traits (**Table S2**). We also modelled cover categories (winners, no change or losers) as a function of the three traits' MTV and ITV in an additive weighted binomial model with a Bernoulli distribution similarly to above.

Statistical models: Distribution models

To understand whether species' absolute and relative ranges were related, we fitted a linear model of absolute versus relative range shifts. To investigate whether species with a larger current range were projected to expand more, we modelled future ranges as a function of current range sizes. We also fitted weighted linear regressions of current range sizes as a function of category (winner, no change or loser), and with median range change (both absolute and relative) as a function of category per individual trait to understand whether species' trajectories were related to smaller or larger present and future ranges (**Table S2**).

Statistical models: Ordinations and analyses of variance

To identify differences between species groups, we performed two Principal Component Analyses (PCAs): one for MTV and another for ITV, using the 'prcomp' function in the R 'stats' package. We centred and scaled log-transformed trait values prior to computing the PCA. We used the R package 'AMR' (Berends et al., 2021) to visualize the trait space for the 36 species for which we had data available on all three traits (including gap-filled species), and plotted the first two component axes. We extracted the PCA scores per species and used them as response variables in linear models against current range sizes, absolute and relative range shifts, and cover change slopes, and we modelled individual PCA scores as a function of winner, loser or no change range category, both for MTV and ITV, and for range and cover species categories.

We performed a permutational multivariate ANOVA test (PERMANOVA) to determine if the different groups (winners, no change or losers) differed statistically in trait space, both for MTV and ITV. We used the ‘adonis’ function in the R package ‘vegan’ (Oksanen et al., 2020) and specified Euclidian distance with 999 permutations. We also calculated average distance to centroids per group with the ‘betadisper’ function in ‘vegan’, and performed an ANOVA test to confirm homogeneity of dispersion among the groups ($p > 0.05$). When the ‘adonis’ analysis yielded a significant difference between categories ($p < 0.05$), we performed pairwise comparisons between them. We used the ‘pairwise.perm.manova’ function in the ‘RVAideMemoire’ package (Hervé, 2020) for 999 permutations and fitted the tests of Pillai, Wilks, Hotelling-Lawley, Roy and Spherical, and specified different methods for p-value adjustment, including Holm and Bonferroni, and with no p-value adjustment. All tests yielded similar significance results. We followed the same methods outlined above for the range and the cover change categories.

Software and model specifications

We used the software and programming language R version 3.6.2 (R Core Team, 2020) for all analyses. We fitted all Bayesian models using the ‘brms’ package (Bürkner, 2017) and ran them for as many iterations as necessary to achieve convergence, which we assessed through examination of the R_{hat} term and trace plots. We considered that there was a clear relationship between variables when the 95% credible intervals of the estimates did not overlap with zero.

Results

Plant trait records were represented across three continents (17,921 records). SLA records were recorded for the most species (*n* = 5,909 records, *n* = 57 species). Plant height records were numerous (*n* = 11,466 records, *n* = 52 species) and widespread geographically, while seed mass records were fewer (*n* = 546 records, *n* = 28 species without and *n* = 40 species with gap-filled data; **Figure 2a, Table S4-6**). By definition, there were differences in plant height values between the different functional groups, with tall shrubs having greater height values than low and dwarf shrubs (**Figure 2b**). In contrast, most of the seed mass median values overlapped across functional groups, and the heaviest seeds belonged to dwarf shrubs (**Figure 2c**). Most median SLA values also overlapped, with both the highest and the lowest median recorded for low shrubs (**Figure 2d**).

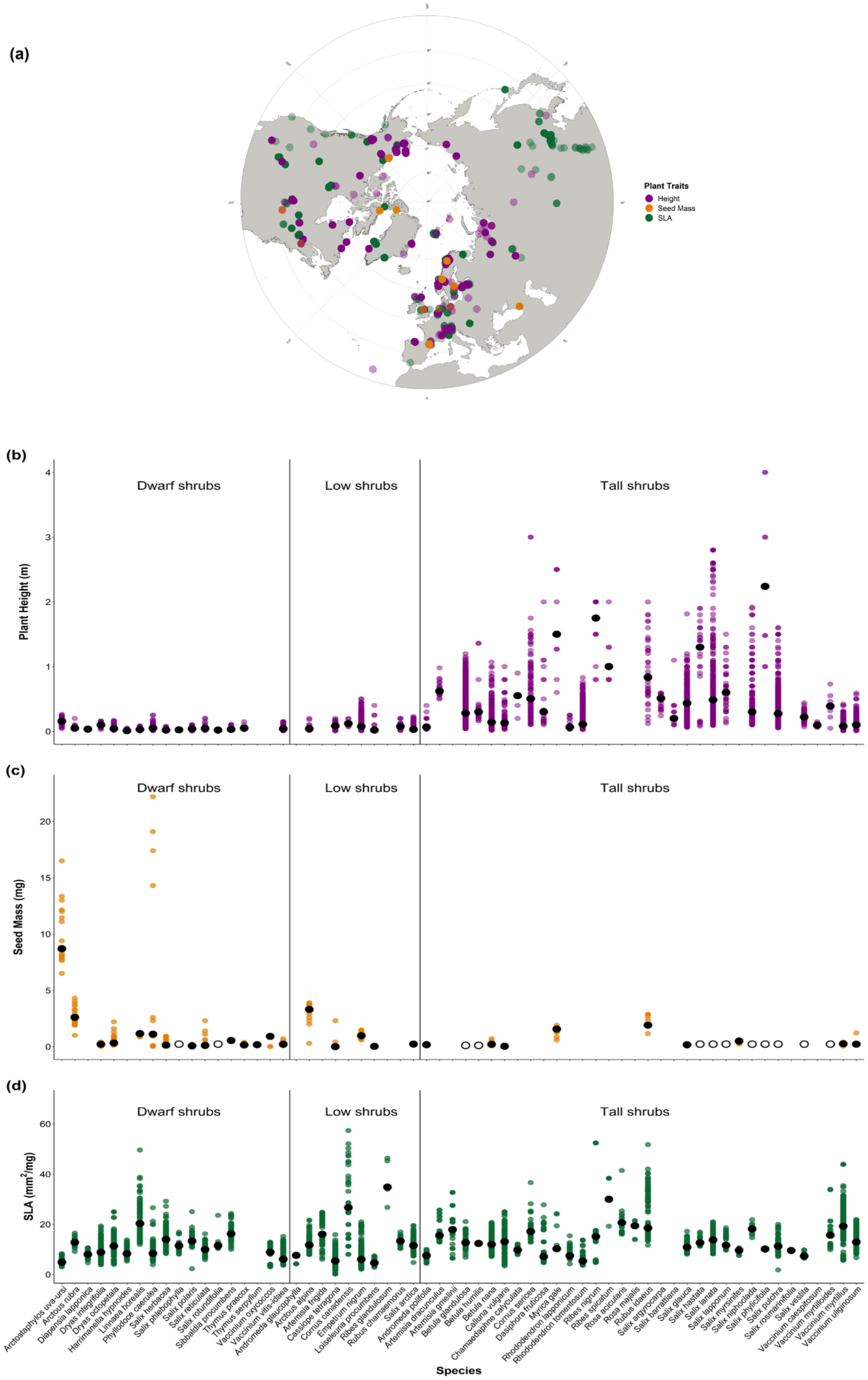
(a)
Plant Traits
Height
Seed Mass
SLA
(b)
Plant Height (m)
Dwarf shrubs
Low shrubs
Tall shrubs
0
1
2
3
4
(c)
Seed Mass (mg)
Dwarf shrubs
Low shrubs
Tall shrubs
0
5
10
15
20
(d)
SLA (mm²/mg)
Dwarf shrubs
Low shrubs
Tall shrubs
0
20
40
60
Arctostaphylos uva-ursi
Arctous rubra
Diapensia lapponica
Dryas integrifolia
Dryas octopetala
Harrimanella hypnoides
Linnaea borealis
Phyllodoce caerulea
Salix herbacea
Salix phlebophylla
Salix polaris
Salix reticulata
Salix rotundifolia
Sibbaldia procumbens
Thymus praecox
Thymus serpyllum
Vaccinium oxycoccos
Vaccinium vitis-idaea
Andromeda glaucophylla
Arctous alpina
Artemisia frigida
Cassiope tetragona
Cornus canadensis
Empetrum nigrum
Loiseleuria procumbens
Ribes glandulosum
Rubus chamaemorus
Salix arctica
Andromeda polifolia
Artemisia dracunculus
Artemisia gmelinii
Betula glandulosa
Betula humilis
Betula nana
Calluna vulgaris
Chamaedaphne calyculata
Cornus sericea
Dasiphora fruticosa
Myrica gale
Rhododendron lapponicum
Rhododendron tomentosum
Ribes nigrum
Ribes spicatum
Rosa acicularis
Rosa majalis
Rubus idaeus
Salix argyrocarpa
Salix barrattiana
Salix glauca
Salix hastata
Salix lanata
Salix lapponum
Salix myrsinites
Salix niphoclada
Salix phylicifolia
Salix pulchra
Salix rosmarinifolia
Salix vestita
Vaccinium caespitosum
Vaccinium myrtilloides
Vaccinium myrtillus
Vaccinium uliginosum
Species

Figure 2. We compiled trait data from shrubs across three continents to test whether trait values and variation were related to range size, projected range shifts and cover change. Trait records with no coordinate information are not represented in the map. **a)** Location of the geo-referenced trait records in this database, north of 30 degrees latitude. Polar projection. **b)** Plant Height values (in m) for 52 species. **c)** Seed mass values (in mg) for 40 species. **d)** SLA values (in mm^2/mg) for 57 species. Each coloured point represents an individual trait value recorded for that specific species. Coloured points are semi-transparent, with darker colour tones indicating overlaps of multiple points. Black points indicate the median value per species. Open black circles indicate the median values of seed mass for gap-filled species. Species are organised alphabetically within functional groups.

We did not find any clear relationships nor interactions between current range sizes and MTV (**Figure 3a, b, c**), nor between current range sizes and ITV (**Figure 3d, e, f**). There were no clear relationships between MTV or ITV and range winner, loser or no change categories. There were also no differences in current range sizes depending on species' dispersal mode, deciduousness, functional group or taxonomic family, except for Salicaceae species having smaller ranges than the Rosaceae family (**Table S2.29**).

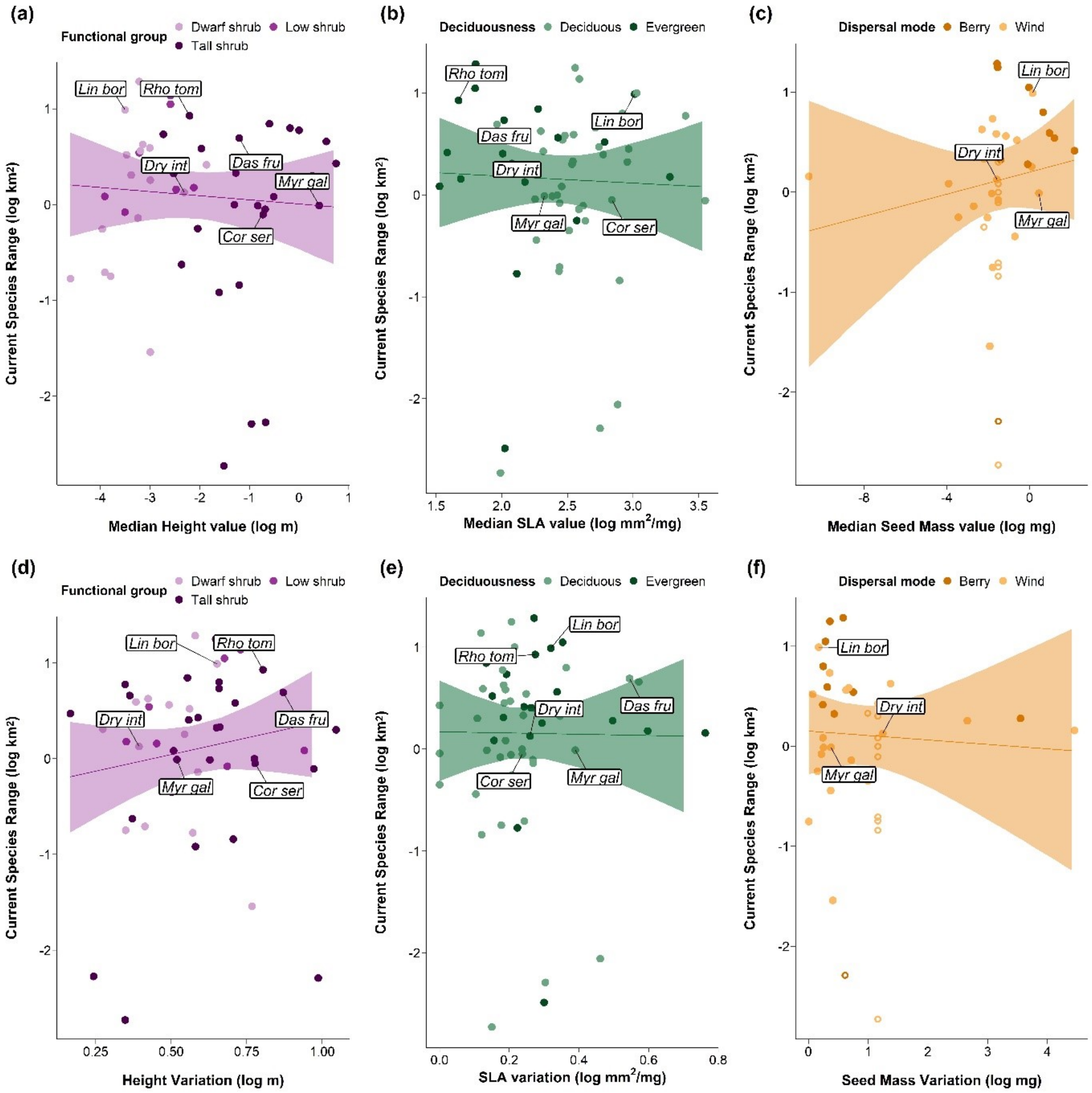

Figure 3. There were no clear relationships between MTV or ITV and current range sizes. Model outputs of the weighted linear regressions of current species range size as a function of **a)** height values **b)** SLA values, **c)** seed mass values, **d)** height variation, **e)** SLA variation and **f)** seed mass variation. MTV are the median per species and ITV is the SD of trait records. Points are raw values and coloured according to categorical traits related to each continuous trait. Lines are the predicted model slopes and the semi-transparent ribbons represent the 95% model credible intervals. Open circles in **c)** and **f)** represent the gap-filled seed mass points calculated from genus

medians. Labels represent abbreviated species as the top three winners (*Rhododendron tomentosum* [previously *Ledum palustre*]*, Dasiphora fruticosa* and *Myrica gale*) and the bottom three losers (*Linnaea borealis, Cornus sericea* and *Dryas integrifolia*).

The projected range shifts method indicated similar numbers of winner (*n* = 28, 45.2%) and loser shrub species (*n* = 26, 41.9%), and fewer no change species (*n* = 8, 12.9%) (**Figure 4**). Among losers, 11 (42.3%) were dwarf shrubs, five were low shrubs (19.2%) and 10 were tall shrubs (38.5%). As for no change species, two were dwarf shrubs (25%), one was a low shrub (12.5%), and five were tall shrubs (62.5%). Among winners, five were dwarf shrubs (17.9%), four were low shrubs (14.3%), and 19 were tall shrubs (67.8%). The winner tall shrubs were also the category-by-functional group combination with the largest number of species in this dataset. All species shared the same range winner, no change or loser category whether considering absolute (**Figure 4a**) or relative range shifts (**Figure 4b**).

In absolute range change terms, top winner species were the tall evergreen shrub *Rhododendron tomentosum*, and the tall deciduous shrubs *Dasiphora fruticosa* and *Myrica gale*. The bottom losers were the dwarf evergreen shrubs *Linnea borealis* and *Dryas integrifolia,* and the tall deciduous shrub *Cornus sericea* (**Figure 4b**). Species' current range sizes and species projected range shifts were related (slope = 118.39, CI = 91.73 to 143.46), and so were median absolute range shifts and median relative range shifts (slope = 55,658.03, CI = 45,319.41 to 65,975.12). Cover change methods identified a majority of no change species (*n* = 19, 52.7%), nine winners (25%), and eight losers (22.2%) (**Table S3**). All functional groups were represented in winner, no change and loser species. Only 10 species shared the same range and cover categories, with four winners, one no change and five loser species in common.

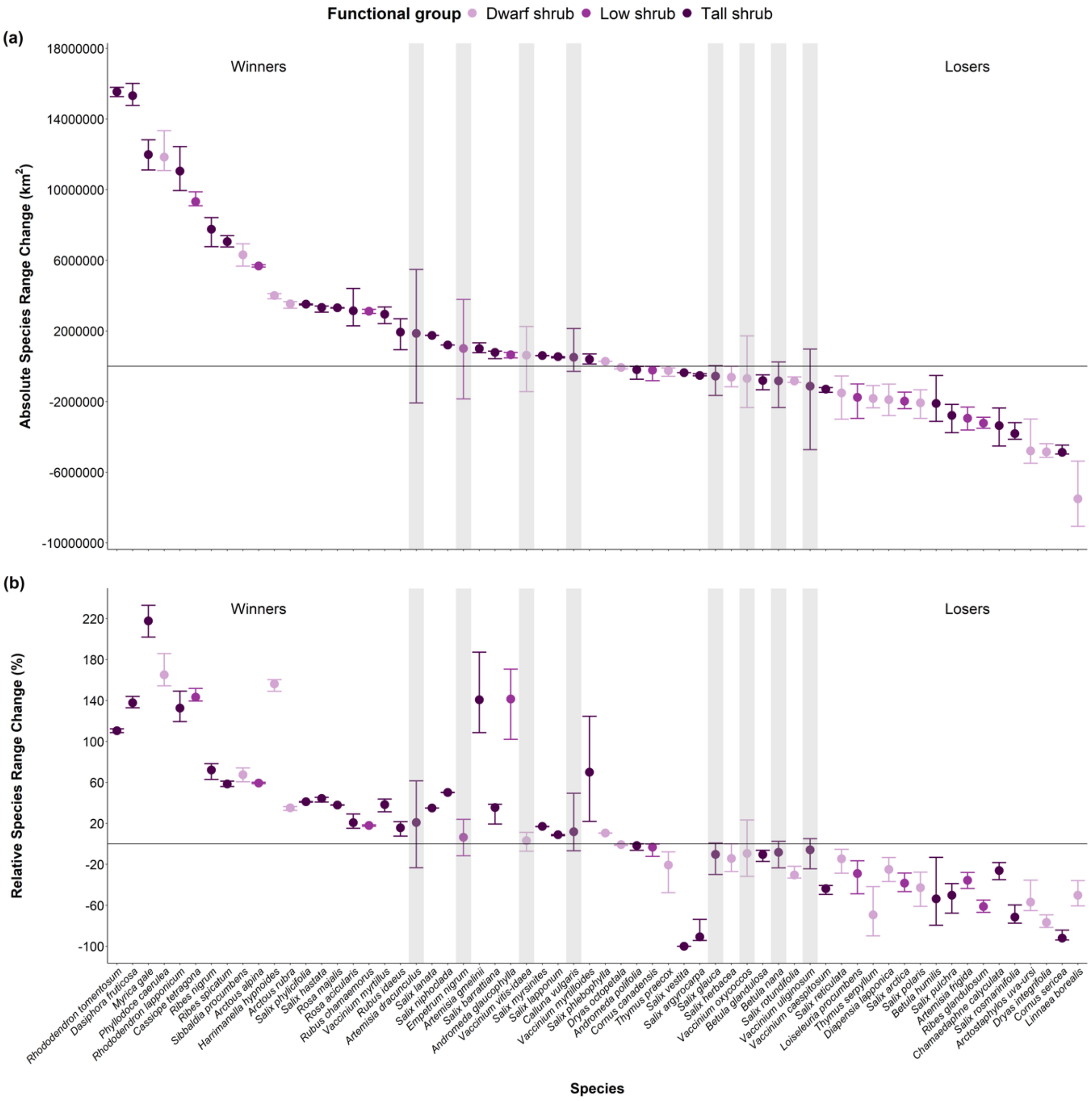

Figure 4. There were similar numbers of winner and loser species on the basis of their predicted species range change in this database for projected **a)** absolute and **b)** relative range change. Each point represents the median across the 24 predicted climatic scenarios per species, while the error bars represent the 25% and 75% quantiles of range change. Species are ordered across the horizontal axis in descending absolute change median value and coloured according to their functional

group. Those species whose lower quantile does not overlap zero are considered winners with expanding ranges, those whose either quantile overlaps zero are considered to experience no change (also indicated by the vertical grey polygons), and those whose upper quantile does not overlap zero are considered losers with contrasting ranges. The horizontal black line represents zero range shift.

Greater seed mass values were associated with greater median absolute range losses in the multivariate model (slope = -0.1, CI = -0.2 to -0.01). There was also a positive interaction between height and SLA for relative median range contractions (slope = 0.6, CI = 0.02 to 1.17), with taller species with greater SLA having greater range contractions. Shrub species with greater SLA variation had greater absolute range shifts (75% quantile, slope = 0.68, CI = 0.1 to 1.25, **Figure S4a**), greater relative range shifts (25%, median and 75% quantile, **Figure S4b, Table S2**), and greater relative range expansions (median, slope = 0.55, CI = 0.08 to 1.03, **Figure S4c**). A 0.5 mm^2/mg SLA variation increase was associated with 18 times greater projected absolute range shifts, double the relative projected range shifts and more than double the relative species expansions (**Figure S4a, b, c**). Species with greater seed mass variation had greater absolute range shifts in univariate models (25%, median and 75% quantiles, **Figure 5f**, **Table S2**). This was also the case when subsetting for wind-dispersed species only (slope = 0.16, CI = 0.02 to 0.29). Note that the median absolute range shift model was only significant for the model including gap-filled species, but not for the model without gap-filled species. Greater seed mass variation was related to median relative range gains (slope = 0.11, CI = 0.01 to 0.21) and absolute range gains (slope = 0.1, CI = 0.002 to 0.2). Range expansions were ~991,273 km^2 larger for each mg of seed mass variation at lower values, with these relationships saturating at higher values of seed mass (**Figure S4d**). We did not find any other relationships between the different MTV (**Figure 5a, b, c**) or ITV (**Figure 5d, e**) and median species range changes. We did not find any relationships between MTV or ITV and winner, loser or no change category. There were also no differences in projected range shifts depending on species' dispersal mode, deciduousness or functional group. However, the Caprifoliaceae family had smaller range shifts than other families, and the Myricaceae family had greater relative range shifts than Salicaceae. We did not find any clear relationships between the slope of average cover change over time and MTV or ITV (**Table S2.134-141**).

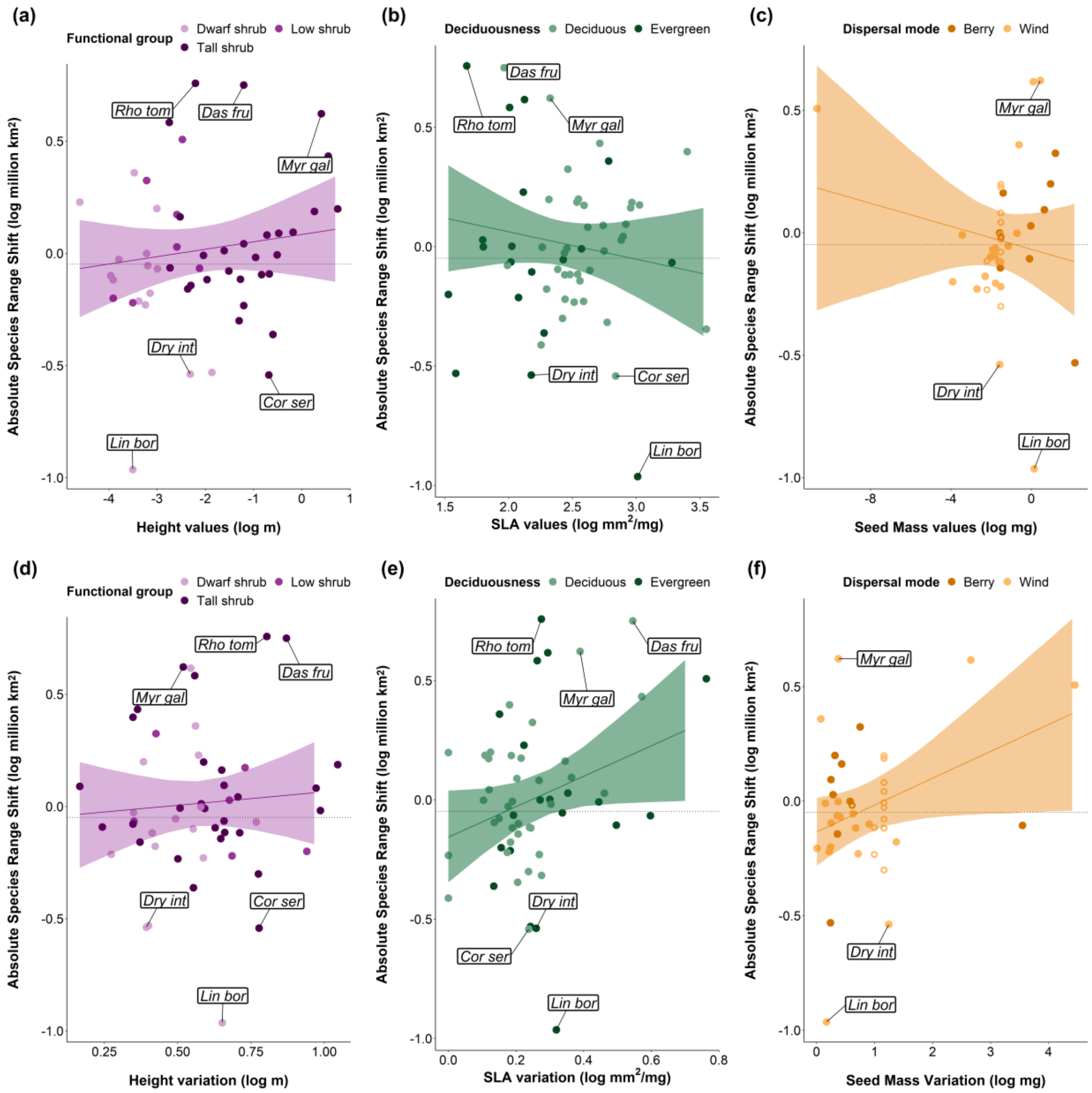

Figure 5. There were no clear relationships between MTV or ITV and median projected range shifts, except for seed mass variation. Model outputs of the weighted linear regressions of median absolute species range change as a function of **a)** height values **b)** SLA values, **c)** seed mass values, **d)** height variation, **e)** SLA variation, and **f)** seed mass variation. MTV represent the median per species and ITV is calculated as SD. Points are raw values and coloured according to categorical traits related to each continuous trait. Coloured lines are the predicted model slopes and the semi-transparent ribbons represent the 95% model credible intervals. Open circles in **c)** and

f) represent the gap-filled seed mass values. Labels represent abbreviated species as the top three winners (*Rhododendron tomentosum, Dasiphora fruticosa* and *Myrica gale*) and the bottom three losers (*Linnaea borealis, Cornus sericea* and *Dryas integrifolia*). Horizontal dotted lines indicate the zero range shift after scaling the data. Species above this line are winners and species below this line are losers.

In the MTV PCA of range categories, no change species were found across the spectrum, losers had medium to low SLA and height values, and winners had greater SLA and height values. PC1 was mainly driven by SLA and seed mass (loadings = 0.65 and 0.6, respectively), and PC2 was driven mostly by height (loading = -0.86). PC1 explained 44% and PC2 explained 30% of the dataset variation (**Figure 6a**). We did not find a significant difference between groups according to the PERMANOVA analysis (*F* = 0.182). There were no significant differences between clusters according to the pairwise comparisons for all tests and p-adjustment methods. We did not find a relationship between range categories and trait values in our binomial model, though plant height was marginally significant (**Figure 6c**).

In the ITV PCA, no change species occupied a small part of the trait space, with medium to high seed mass and SLA variation, but medium to low height variation, while losers occupied a larger part of the trait space. Winners occupied the largest trait space for all three traits, and those species with higher variability in plant height were winners. PC1 was mainly driven by seed mass and SLA (loadings = 0.68 and 0.63, respectively), and PC2 was driven mostly by plant height (loadings = -0.91). PC1 explained 49% and PC2 explained 31% of the variation in the dataset (**Figure 6b**). We did not find a significant difference among clusters in the PERMANOVA test (*F* = 0.4), but winner clusters where slightly different to no change clusters (Tukey test of multivariate dispersions, *p* = 0.049). Further, in our binomial model greater seed mass variation was more likely to correspond to winners (slope = 1.47, CI = 0.09 to 3.27; **Figure 6d**). PC2 component scores had a negative relationship with relative range shifts (**Table S2.154**), but we did not find any other clear relationships when modelling current range sizes, absolute range changes and relative range changes as a function of PC1 and PC2 component scores, for either MTV or ITV. We did not find differences either in winner, loser and no change categories for PC1 and PC2 scores, neither for MTV nor ITV.

Species categories based on cover change overlapped largely in the MTV PCA, with losers having the larger trait space (**Figure S5a**). PC1 was driven by SLA and seed mass (loadings = 0.7 and 0.57, respectively), while PC2 was driven mostly by plant height (loading = -0.8). PC1 explained 41% and PC2 explained 33% of the dataset variation. In the ITV PCA, clusters of loser and winner species overlapped, though winners had greater height variation (**Figure S5b**). PC1 was driven mostly by SLA and seed mass (loadings = 0.66 and 0.65, respectively), and PC2 by plant height (loading = -0.92). PC1 explained 55% and PC2 explained 29% of the dataset variation. In both PCAs, we did not find a significant difference among winner, loser and no change clusters in the PERMANOVA test, in the binomial models, nor when modelling mean cover change over time as a function of PC1 and PC2 component scores.

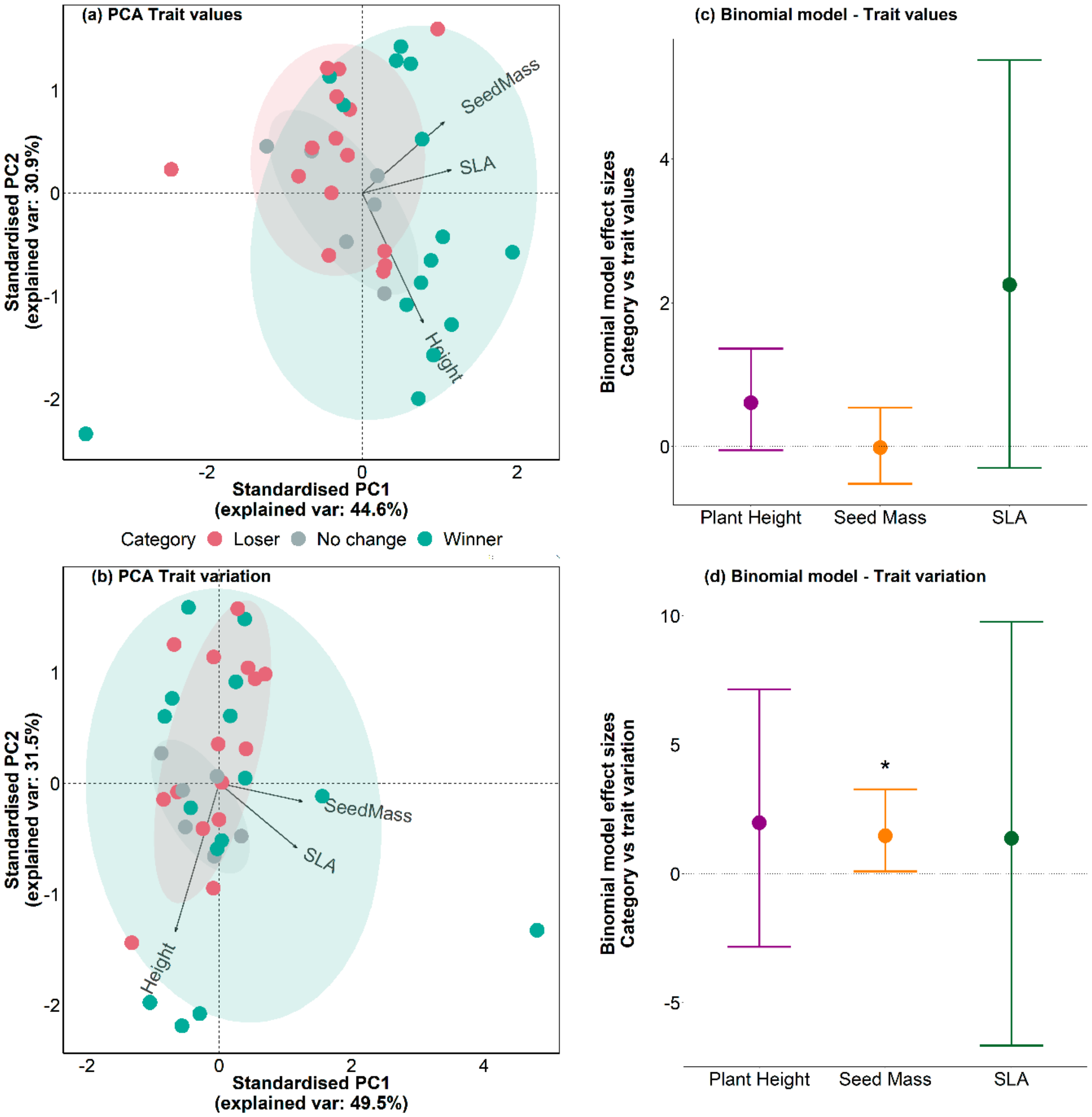

Figure 6. Range winners had slightly different trait values from loser and no change species. Principal Component Analysis for **a)** MTV and **b)** ITV (*n* = 36). Ellipses and points are coloured according to species categories. Arrows indicate direction and weighting of each trait. Ellipses indicate the 68% confidence interval of distributions per category. **c)** and **d)** Effect sizes of the binomial models with category (winners versus losers and no change) as a function of **c)** MTV and **d)** ITV. Mid-points represent mean posterior estimates and vertical error bars represent the 95% credible intervals

of the slope estimates. Asterisks indicate relationships between categories and traits that did not overlap zero (represented by the horizontal dotted line).

Discussion

Species' range expansions/contractions and abundance increases/decreases are forecasted with climate change. In this study, winner species were more likely to have greater seed mass values, and greater variation in SLA and seed mass compared to losers, potentially conferring an advantage in a warmer future climate. However, the relationship of MTV and ITV with projected range shifts was highly dependent on the range shift quantiles considered per species (**Table S2**). Contrary to our hypotheses, specific values of continuous traits (e.g., shorter stature) and groups within categorical traits could characterize both winner and loser species. Additionally, species projected through SDMs to expand their ranges are not the same species that have increased in cover over time, showing a mismatch when employing different assessment methods. Species' projected range shifts may have consequences for the future trait composition of tundra communities (Bjorkman, Myers-Smith, et al., 2018), but not in mechanistic ways given that winners and losers share moderately similar trait spaces.

Winners and losers in a warming Arctic

Range winners tended to have greater seed mass values than no change and loser species, though not in a consistent manner. Plant height, SLA and seed mass are important response traits which are sensitive to climate change and thus influence species' abilities of persisting in and colonise changing habitats (Baruah et al., 2017). Thus, we expected tall shrubs with greater SLA to be winners due to their increased competitive ability, but contrary to our expectations, heavier seeds seemed to relate to range shifts more than lighter seeds. Plants with lighter seeds tend to disperse further and produce more seeds (Hamilton et al., 2005; MacLean & Beissinger, 2017), but larger seeds are more likely to be within berries that are dispersed by animals over longer distances (Nathan et al., 2008). Moreover, large seeds are at an advantage when it comes to seedling establishment due to more storage tissue (Hamilton et al., 2005; Moles & Westoby, 2004), thus suggesting seed mass is not a reliable predictor of range processes. Under climatologically favourable conditions, tall shrubs and those with greater SLA have a competitive advantage over other species (Gaudet & Keddy, 1988), and the height of tundra plants has increased with warming over the past few decades (Bjorkman, Myers-Smith, et al., 2018). Tall plants may expand with increasing solar radiation and rainfall (Moles et al., 2009, Pollock et al., 2012,), but similar climatic conditions support communities with different MTV, and different climates can support communities with similar MTV (Bruelheide et al., 2018). Therefore, while macroclimate might link well with community trait values, individual trait values and ITV could instead be more affected by microclimate, including factors like topography, soil moisture and nutrients (Lembrechts et al., 2018; Opedal et al., 2015). While taller species represent more winners than shorter species, which tended to be losers (**Figure 6a**), this climate-trait mismatch could mean that tall shrubs will not necessarily take over the landscape, as frequently reported in tundra projections.

Surprisingly, only 10 of the 36 shrubs (27.7%) with data on cover change over time shared the same winner/loser categories as the species range categories, with four winners, one no change and five loser species in common (**Figure 4, Table S2, Figure S3**). This result does not support the generally accepted abundance-range size theory (Gaston & Blackburn, 2008), but agrees with other studies (Sporbert et al., 2020). A potential explanation is that the SDM-derived ranges identify potential future climatic niches constrained by boundaries set by species-specific migration rates, rather than the real-world climate responses of tundra shrubs. For instance, a species could be classified as a winner because of an expanded climatic niche, but as a loser because of decreased cover change, meaning that its fundamental niche does not track its potential future climatic niche. Conversely, a species may be classified as a loser because of a projected range contraction, but be able to persist *in situ* and adapt to changing climatic conditions, which SDM projections would not be able to capture.

The environmental factors affecting broad geographical extents likely differ from those affecting local scale abundances (Sporbert et al., 2020). Additionally, range shifts are contingent on geographical context, and species responses might differ depending on the space available for expansion (e.g. in North America versus Scandinavia). Moreover, biotic interactions (e.g. competition, herbivory) at local scales dictate the realization of potential climatic niches (Kaarlejärvi et al., 2017; Maliniemi et al., 2018). Topography also influences plant growing conditions through numerous geological and hydrological processes and has been shown to improve SDM predictive ability (Mod et al., 2016). This complexity highlights the challenges in estimating plant responses to warming where abundance increases may not translate directly into range expansions derived from SDM approaches.

Plant traits are not strongly related to species ranges or abundance

While traits have been extensively linked to predicting plant success, we found that the traits used in this study were weakly related to the projected range shifts and past cover change of tundra shrubs (**Figure 5**). Previous studies have yielded similar results: habitat availability was more relevant than selected traits as range shift predictors for Swiss alpine plants (Angert et al., 2011), seed mass or plant height and area were not related in herbaceous plants in Swedish forests (Dupré & Ehrlén, 2002), and neither seed mass nor plant height predicted current species ranges for European plants (Estrada et al., 2015). Likewise, a global meta-analysis and a systematic review found no significant effect of traits (apart from habitat breadth and historic range limit) on range shifts (Beissinger & Riddell, 2021; MacLean & Beissinger, 2017), and indeed we found a strong positive association between current range sizes and projected range shifts (**Table S2.35**). Moreover, there is some evidence of poor trait predictive ability of long-term ecosystem properties, plant-environment relationships, and vital rates (Kremer et al., 2014; Salguero-Gómez et al., 2018; van der Plas et al., 2020). Together, these results indicate that contrary to our hypotheses and previous studies (Cornwell & Ackerly, 2010; Veken et al., 2007), these three key plant traits are not consistently associated with projected climate-induced range shifts.

Range shifts and cover change were also not defined by categorical traits such as taxonomy, dispersal mode, deciduousness or functional group (**Table S2.126-133**). We expected the *Salicaceae* or *Betulaceae* families to be the greatest winners given their reported increases across tundra ecosystems (Bjorkman, Myers-Smith, et al., 2018; Elmendorf et al., 2012; Myers-Smith, Forbes, et al., 2011), but our family sample size was potentially too small to detect a taxonomic signal. Although wind-dispersed (anemochorous) seeds generally have greater migration rates than animal-dispersed (zoochorous) seeds (Holzinger et al., 2008), we did not find anemochorous species to have larger current or projected ranges than zoochorous species. Thus, both wind and animal dispersion might facilitate long-distance dispersal, or other factors like vegetative propagation or seed viability might be more relevant in explaining dispersal (Aubin et al., 2016), but the limited number of species with seed data limits our ability to make broad generalisations. Deciduous shrubs have been identified as the group expanding the most with tundra warming due to rapid resource acquisition thanks to leaf turnover (Elmendorf et al., 2012; Prager et al., 2020), but evergreen shrubs are also increasing as they seem to be more responsive to warming than originally thought (Hudson et al., 2011; Vowles & Björk, 2019; Vuorinen et al., 2017), and our analyses showed no range differences related to species deciduousness. All functional groups are expected to be represented in a warming tundra (Chapin et al., 1996), and they represent variation within traits very coarsely, with large overlaps in trait values between groups (Betway, Hollister, May, & Oberbauer, 2021; Thomas et al., 2019). These overlaps were thought to be due to ITV, and indeed we found an indication that species with greater SLA and seed mass variation are projected to expand the most, suggesting that winner species are more plastic or have greater potential to adapt to changing environmental conditions due to within-population genetic variation (Bolnick et al., 2011). However, these results were far from consistent and support the general finding that tundra species will have highly individualistic and heterogeneous responses to climate change (Bjorkman et al., 2019; Hollister et al., 2005; Myers-Smith et al., 2020; Thomas et al., 2019).

Beyond functional traits

Our initial hypothesis of tundra shrubs showing similar trait responses to climate change turned out to be too simplistic. This weak relationship between traits and ranges might be attributable to different factors. First, the species' projected range shifts might be related to traits reflecting specific dispersal and colonisation processes not captured by the selected traits; thus a different suite of morpho-physiological traits underpinning climatic preferences might have more explanatory power, such as leaf, stem and root density, C, N and P contents, and cold hardening (Díaz et al., 2016; Harrison et al., 2010; Kühn et al., 2021). Similarly, different traits might be more related to local abundance than to projected range shifts. Second, there are intrinsic differences in life history and physiology that are not accurately captured with these particular traits or by one-time measured traits only (Hamilton et al., 2005; Volaire et al., 2020). Third, SDM range projections may only quantify part of the full species climatic niche due to the limitations in predictor data (e.g., uncertainties in climate predictions, lack of soil temperature, moisture or nutrient data) and to potential bias in the input occurrence data caused by sampling bias, biotic interactions, and long-term dispersal limitations (Svenning et al., 2011). Fourth, SDM projections were constrained by species-specific migration rates to avoid overestimating range shifts, but uncertainties remain regarding the influence of biotic interactions on future range shifts (Gough, 2006; Pearson & Dawson, 2003; Post et al., 2021; Wisz et al., 2013). However, in the absence of long-term monitoring studies of traits and range shifts over time, SDM-derived projections are the best spatial data currently available to test these questions.

The relationships among traits and range shifts could be influenced by other factors not addressed in this study. Phenology change (e.g., extended growing season length) can buffer climatic impacts or alter species' survival and reproduction, for example through greater temperature sensitivity in late-flowering species (Prevéy et al., 2019). Future studies are needed on phenology as a trait influencing tundra plant responses to climate change. Heterogeneity is expected in permafrost thawing rates and soil deepening across tundra habitats, resulting in different amounts of nutrient availability and consequent effects in plant trajectories (Mekonnen et al., 2018). Similarly, examining the influence of microclimate, topography and edaphic conditions could be an important next step to better understand distribution shifts (Hylander et al., 2015). Finally, demographic processes not captured by the traits investigated in this study might be determining the success of species range shifts more directly.

The filtering role of demographic processes such as survival, fecundity, germination and establishment might affect range shifts more than traits per se (Hemrová et al., 2017; Normand et al., 2014). Demographic processes might be more relevant than dispersal in the tundra given the substantial role of microclimate in defining species reproduction, but they are much harder to measure than traits (Graae et al., 2018). Although long-distance colonisation is common in the Arctic, multiple successful recruitment events are needed for a species to expand into a new area (Alsos et al., 2007). Establishment might limit distributions more than dispersal, with establishment being in turn determined by the number of viable seeds and the environment (Lenoir et al., 2012). Both environmental conditions and biotic interactions such as herbivory and both intra- and inter-specific competition can heavily affect demography (Ehrlén et al., 2016; Gough, 2006). Further research is needed on how demography influences tundra shrub distributions to understand if demographic rates could prove to be more powerful predictors of climate change-induced range shifts than dispersal traits (Hemrová et al., 2017; Salguero-Gómez et al., 2018).

We worked under the assumption that MTV and ITV will remain constant over time, but there is an indication that plant height, leaf area and seed mass will change with climate change (Bjorkman, Myers-Smith, et al., 2018; Myers-Smith, Grabowski, et al., 2019). With repeated tundra trait data being rarely collected over time (Bjorkman, Myers-Smith, et al., 2018), we included species records outside of the tundra to account for trait plasticity and the likelihood of tundra trait values shifting in the future (Thomas et al., 2020). We suggest that the collection of repeated trait data could improve our understanding of individual and community trait change over time. Similarly, geographical coverage in TRY/TTT across the Arctic is incomplete (**Figure 2a**) and trait data were not available for all species with distribution data (**Figure 2b, c, d**). Species with no trait data might be precisely those which are endemic or rare, and potentially experiencing range contractions, leading to an overall under-representation of rare species. Further trait data collection across the Arctic would help overcome the under-representation of particular traits and species, and enable the replication of these analyses based on a larger number of morpho-physiological traits.

With range change data over time not yet available, SDM projections remain the only current way to estimate range dynamics. Projections provide a proxy for potential range shifts, and the relationships we found partly reflect the assumptions made when calculating SDMs. These SDM models did not consider other environmental variables beyond temperature and precipitation, and we found strong differences in projected range shifts between the 24 different climatic scenarios. Once range change data over time becomes available (e.g., through the GLORIA or MIREN networks), the relationship between observed range shifts and traits could be further explored, and SDMs can be validated against on-the-ground observations. Additionally, we chose to examine ranges on the basis of traits because we were interested in the potential explanatory power of traits as proxies for species distributions, but the influence of projected range shifts on MTV and ITV could equally yield interesting results.

Earth system models (ESMs) assume high uncertainty (Bonan & Doney, 2018) and usually simplify diverse plant communities using functional types parametrised with summary trait values (Fisher et al., 2018; Wullschleger et al., 2014). However, our findings suggest that plant traits poorly explain variation in tundra species distributions, and that different methods result in different categories of winner and loser tundra shrub species. While acknowledging that moving beyond broad functional types will increase model complexity (Fisher et al., 2018), we advocate for ESMs to incorporate trait variability, together with demographic processes. Progress is already underway through the definition of Arctic-specific functional groups and the inclusion of certain traits on Earth Land Models, improving overall projections (Sulman et al., 2021). In order to more accurately project tundra vegetation shifts, incorporating the real-world complexity inherent in the diverse tundra shrub responses to a warming climate remains crucial.

Conclusions

Our findings indicate that no specific combination of trait values or variation is associated with winner or loser tundra shrub species under climate change. Contrary to our expectations, particular trait values or greater trait variation do not necessarily indicate increased range or abundance shifts, although there was a broadly positive signal of greater seed mass values with projected range shifts, and greater SLA and seed mass variation with projected range shifts. Overall, we observed similar values of height, SLA and seed mass for both range expanding and contracting tundra shrub species. Thus, projected range shifts will not lead to directional shifts in shrub trait composition or variation, as both winner and loser species share a relatively similar trait space. Additionally, winner and loser species differ when comparing past cover change over time with projected range shifts. Future research could investigate the explanatory power of other morpho-physiological traits and address how demographic processes might mediate tundra shrub range shifts. Our results demonstrate that tundra shrubs can be equally resilient or vulnerable even with very different combinations of trait values and variation. Identifying the future winners and losers of climate change in the tundra biome remains a complex endeavour, but these results outline that the wide variety of evolutionary strategies that tundra plants employ are not necessarily reflected in their responses to a warming climate.

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