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RESEARCH ARTICLE

The relationships of plant species occupancy to niches and traits vary with spatial scale

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Abstract

Aim: Support for different underlying mechanisms of species occupancy is inconsistent, yet this could be related to spatial scale. Since abiotic filtering typically acts at broader scales than biotic interactions, we hypothesise that occupancy could be more driven by species' abiotic niche (i.e. tolerance and preference of abiotic conditions) at broad scales, whereas species' traits affecting competitive ability could be more important at fine scales. Here, we test these hypotheses by assessing relationships of occupancy to niche and trait metrics across spatial scales.

Location: Four study areas located north of Arctic Circle.

Taxon: Vascular plants.

Methods: We derived occupancy for 106 species at four spatial scales (micro-scale with plot size of $0.04\,m^2$ and extent of 2km, local-scale with plot size of $4\,m^2$ and extent of 40km, regional-scale with plot size of 4ha and extent of 800km, and polar-scale with plot size of $4\,km^2$ and extent of 5200km). We then assessed using generalized additive models whether the relationships between occupancy and species' niche breadth, niche marginality, intraspecific trait variability (ITV) and trait distinctiveness vary across the scales.

Results: At the finer scales, ITV (especially of specific leaf area) had the highest contribution with positive relationship in explaining occupancy. At the broader scales, occupancy was better explained by niche metrics. Especially at the broadest scale, the occupancy had a positive relationship with species' climatic tolerance.

Main Conclusions: Abiotic filtering, especially related to macro-climate, drives species occupancy at broader spatial scales while biotic interactions are relatively more important at local scales. This scale-dependency of factors behind species occupancy should be accounted for when, for example, planning conservation of rare species, forecasting invasions or anticipating the effects of changing climate on biota at local versus global scales.

KEYWORDS
abiotic filtering, Arctic, biotic interactions, high-latitudes, prevalence, rarity, scale-dependency, vegetation

1 | INTRODUCTION

Some species occur more frequently across space than others, but why? Species occupancy (i.e. occurrence frequency) reflects species' rarity versus commonness and can be derived as the count of locations where a species occurs in an area (Flather & Sieg, 2007; Gaston, 1994). Occupancy has been linked to a multitude of ecological drivers, such as habitat and resource availability and use, vital rates of populations, and dispersal (Bevill & Louda, 1999; Borregaard & Rahbek, 2010; Gaston et al., 1997; Kunin & Gaston, 1993). However, despite the long history of studies on the topic, consistent support for different underlying mechanisms has not been found. Understanding the mechanisms behind species occupancy would be crucial, for example, to maintain biodiversity supported by rare species (Williams et al., 2009), to target conservation efforts (Giam & Olden, 2018), to identify invasive species (Fristoe et al., 2021), and to anticipate species vulnerability (Broennimann et al., 2006) and successful adaptations under changing climate (Monaco et al., 2020).

The mechanisms behind species occupancy can be divided to deterministic (abiotic filtering and biotic interactions) and stochastic (e.g. dispersal and ecological drift; Chase & Leibold, 2003). At the species-level, the deterministic mechanisms are related to species' abiotic niche and traits (Borregaard & Rahbek, 2010; Heino & Tolonen, 2018). For vascular plant species, abiotic niche describes the abiotic environmental conditions where a species can establish and persist as viable population, and thus, partly defines its geographic distribution (Holt, 2009; Hutchinson, 1957; Pulliam, 2000). Traits, in turn, describe morphological, physiological or phenological features of individual organisms used to reach, perform and compete in a locality (Violle et al., 2007). Consequently, metrics derived using species' abiotic niche and traits can be used to indicate the mechanisms behind occupancy.

First, a species' occupancy could be affected by its capacity to tolerate a range of abiotic conditions, that is, its *niche breadth* (NB; Slatyer et al., 2013). The assumption is that species with large NBs occur more frequently in an area as they can occupy a wider range of abiotic conditions than species with narrow NBs. Second, a species' occupancy could be affected by the availability of its preferred habitat in an area (Venier & Fahrig, 1996). The species, which occupy common habitats, could have higher occupancy than the species, which occupy the marginal habitats. Thus, *niche marginality* (NM; i.e. the difference between species' niche position and median abiotic conditions of an area; Hirzel et al., 2002) should have a negative relationship with species occupancy. Third, a species with high *intraspecific trait variability* (ITV; Bolnick et al., 2011; Westerband et al., 2021) could have higher occupancy by having advantage to adapt to (Violle & Jiang, 2009) and/or compete in diverse abiotic and biotic conditions (Bennett et al., 2016). Fourth, the traits themselves could also affect species occupancy. On the one hand, species with similar traits are expected to prefer abiotically similar areas (i.e. habitat filtering; Keddy, 1992) resulting in species with distinctive (i.e. unsuitable to the abiotic conditions) traits being rare. On the other hand, the species occupying the same location are exposed

to competition, resulting in species with distinctive traits possibly having higher occupancy due to competitive advantage (Szabó & Meszéna, 2006). Species' *trait distinctiveness* (TD; i.e. how different a species in average is from other species; Marino et al., 2020) could thus affect species occupancy either negatively or positively.

Studies investigating the roles of abiotic niche and traits have found more support for niche determining species occupancy (e.g. Boulangeat et al., 2012; Heino & Grönroos, 2014; Marino et al., 2020; Rocha et al., 2018). Heino and Tolonen (2018) suspected that this outcome could be partly related to spatial scale (see also Borregaard & Rahbek, 2010; Brändle & Brandl, 2001; Hartley et al., 2004). Despite the fact that niche and traits are inherently connected by both describing species' ability to perform in relation to abiotic and biotic environment (Fajardo & Siefert, 2019; Sides et al., 2014; Treurnicht et al., 2020; Violle & Jiang, 2009), certain traits, such as height, specific leaf area (SLA) and seed mass, are more directly linked to species competitive ability than niche (Jakobsson & Eriksson, 2000; Kunstler et al., 2016; Sporbert et al., 2021). Thus, trait metrics might be more decisive at fine spatial scales (meaning here small extents and grain sizes) where species interact (Araújo & Rozenfeld, 2014). In contrast, preference and tolerance of abiotic conditions (i.e. abiotic niche metrics) could be more related to occupancy at broader scales (meaning here large extents and grain sizes), since abiotic filtering typically acts at broader scales (Lortie et al., 2004) and environmental variation increases with spatial extent (Slatyer et al., 2013). Scale-dependence could also affect the relationship between occupancy and TD (Scherrer et al., 2019). At finer scales, distinctive traits could be an asset in competition with neighbouring species (Szabó & Meszéna, 2006) leading to a positive relationship. At broader scales, abiotic filtering would lead to species with more similar traits and, thus, to a negative relationship between TD and occupancy.

Spatial scale could thus affect the importance of different mechanisms behind occupancy and explain the varying occupancy of species across scales (He & Condit, 2007; McGeoch & Gaston, 2002). For example, large NB could be more beneficial for occupancy at broad than at fine scale, where high ITV and TD could be relatively more beneficial. Examining the drivers and their scale-dependencies would assist, for example, in identification of invasive species at local versus global scales (Mack et al., 2007) and targeting conservation actions of species to correct spatial scale (Boyd et al., 2008; Hartley & Kunin, 2003).

Thus, here, we examine whether the relative importance of niche versus trait metrics in explaining species occupancies varies with spatial scale. We utilize occurrence information of 106 vascular plant species collected from four nested study areas with different extents and resolutions north of Arctic Circle. Under the assumption that the niche mostly describes species tolerance and preference for abiotic conditions and the used traits additionally capture species competitive ability, our hypothesis is that the trait-related metrics better explain occupancy at fine than at broad scales where the niche metrics, in turn, are relatively more important. We further test whether the niche (NB and NM) and trait metrics (ITV and TD)

based on different environmental dimensions (e.g. climate) or traits (e.g. height) better explain occupancy across scales.

2 | MATERIALS AND METHODS

### 2.1 | Species occupancy at different spatial scales

To differentiate species occupancy across spatial scales, we collected vascular plant species occurrences from four nested study areas with different extents and resolutions (Turner et al., 1989; Figure 1). All study areas are located north of Arctic Circle (66.5°N) and represent tundra environment from forest line to (oro-)arctic desert. To avoid incorrect species identifications across scales, the species with ambiguous taxonomy (species of *Alchemilla*, *Hierachium*, *Pilosella* and *Taraxacum* genera apart from *A. alpina*) and hybrid taxa from genus *Salix* were not included, and species names were compared and harmonized against GBIF Backbone Taxonomy (GBIF Secretariat, 2019). The excluded taxa do not constitute a large portion of vegetation in the high-latitudes. For example, out of the 573 sites at the local scale, *Alchemilla* species (apart from *A. alpina*) were found at 37 sites (with mean cover of 0.8%), *Hieracium* and *Pilosella* species at 246 sites (with mean cover of 0.2%) and *Taraxacum* species at 81 sites (with mean cover of 0.5%). At all scales, occupancy of each species was calculated as the sum of plots/sites/grid cells (depending on the scale; see below) where the species is present, and occupancies were then scaled between 0 and 1000 (0=no occurrences, 1000=highest occupancy).

At the finest scale (hereafter called micro), species occurrences were surveyed from 1920 square plots (20×20 cm) in northern and southern slopes of Mount Saana in Northern Finland (69.04°N, 20.86°E) during summers 2011–2012. Plots were organized in 12 grids (8×20 m) with minimum and maximum distances among plots being c. 0.5 m and 2.5 km, respectively. The grids were located

approximately at same elevation (700 m a.s.l.) to cover the different mesotopographic conditions (e.g., moist hollows, windswept dry ridges, geomorphologically active slopes and undisturbed flats) and typical habitats of the study area (e.g. *Empetrum* heaths, meadows, nivations; le Roux et al., 2014).

At the next finest scale (local), the data consist of 573 sites with pooled occurrences surveyed from four 1 m^2 plots located 5 m from the centre of each site (Mod, Heikkinen, et al., 2016). Study area is located in northern Finland and Norway (68.75–69.34°N, 20.74–21.30°E), with minimum and maximum distances among the sites being c. 50 m and 65 km, respectively. The locations of the sites were chosen to represent the different elevations (460–1360 m a.s.l.) and typical habitats (e.g., treeline formed by *Betula pubescens* subsp. *czerepanovii*, *Empetrum* heaths, meadows, nivations and blockfields) of the study area. Vegetation survey was done 2008–2013.

At the next scale (regional), the study area covers mainland areas of Finland, Sweden and Norway north of Arctic Circle (c. 250,000 km^2). Occurrences of the species found at the local scale—under an assumption that these species comprehensively represent typical vegetation of the study areas—were derived for this study area from GBIF database (GBIF.org [29 March 2020] GBIF Occurrence Download https://doi.org/10.15468/dl.nolkaq) and complemented with entries from national databases of Finland (https://laji.fi/en), Sweden (https://www.artportalen.se/) and Norway (https://www.artsdatabanken.no/). We included only occurrences that were surveyed 1990–2019 and contained information of location accuracy and where the accuracy was at least 100 m. Occurrences with duplicate coordinates per species and the occurrences falling to sea or on a glacier were removed. Species occurrences (296,223 after cleaning the data) were then aggregated to a grid with 200 m resolution [using functions in the R-packages 'raster' (4.3; Hijmans, 2021) and 'sp' (1.4; Bivand et al., 2013; Pebesma & Bivand, 2005)] to mimic the per plot occurrences at micro and local scales and resulting in 33,000 grid cells with at least one occurrence of one species.
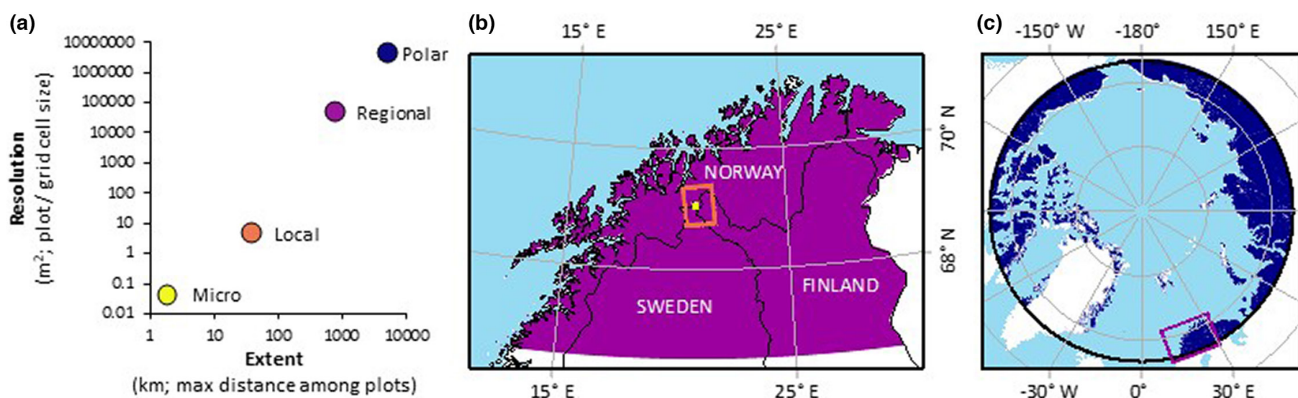
FIGURE 1 Extents (km; max distance among plots/grid cells), resolutions [m^2; plot/grid cell size; (a)] and locations (b, c) of the four nested study areas north of the Arctic Circle that were used to derive occupancy of 106 vascular plant species. The location of the study area at micro scale and the extent of the study area at local scale are marked with yellow and orange squares, respectively, in (b). The study area at regional scale covers Finland, Sweden, and Norway north of Arctic Circle [in purple in (b, c)] and the study area at polar scale covers all terrestrial non-glaciated area north of Arctic Circle [in blue in (c)]. Projections in the maps are Transverse Mercator with central meridian 21°E (b) and Lambert Azimuthal Equal Area (c).

Comparison of temperature conditions of these grid cells and those of the total study area indicated sampling bias towards warmer conditions (Figure S1). Thus, we performed environmental thinning (Inman et al., 2021), meaning a random removal of grid cells with species occurrences so that the distribution of temperature conditions matched with those of the total study area, resulting in ~27,500 grid cells used to calculate occupancy at this scale.

At the broadest scale (polar), the study area is all terrestrial non-glaciated area north of Arctic Circle. Occurrences of the species for this study area were derived, cleaned and thinned as at the regional scale, except using only GBIF database (GBIF.org [14 April 2021] GBIF Occurrence Download https://doi.org/10.15468/dl.hvb7xm), allowing the entries that had a coordinate accuracy of at least 1km and were surveyed 1990–2020, and aggregating the occurrences to a grid with ~2km resolution. At this scale, warm grid cells (mean annual temperature [MAT] > −5°C) were overrepresented too, whereas the occurrences from the coldest grid cells (MAT < −15°C) were almost completely lacking (Figure S2). While the overrepresentation of warm locations likely represents sampling bias, the low number of records from cold conditions could, instead, represent a real lack of vegetation. At this scale, the environmental thinning was, thus, targeted only to grid cells with MAT > −5°C. We removed randomly as many grid cells as possible without losing all occurrences of any species, resulting in using ~3000 grid cells of the original ~15,000 to derive the occupancies.

2.2 | Niche metrics

Niche breadths (NB; a measure of abiotic tolerance; see Figure 2) and marginalities (NM; a measure of abiotic habitat availability)

for the species were derived using global species occurrences and environmental conditions to avoid spatial niche truncation (Thuiller et al., 2004). Following the procedures of deriving and cleaning the data at regional and polar scales, the species occurrences were derived from the GBIF database (GBIF.org [14 April 2021] GBIF Occurrence Download https://doi.org/10.15468/dl.hvb7xm), but allowing entries that had a coordinate accuracy of at least 10km. To reduce sampling bias, occurrences of each species were spatially thinned (utilizing the R-package 'spThin' 0.2.0; Aiello-Lammens et al., 2015). Following the work of Fourcade et al. (2018), we accounted for the varying range sizes of species by choosing a thinning parameter (i.e. the minimum distance among occurrences) per species as the maximum distance among the occurrences divided by a constant. A constant of 200 resulted in, for example, a thinning parameter of ~100km for the species with global distribution and a thinning parameter of ~10km for the species with Scandinavian distribution. This was considered adequate to remove the spatial bias while retaining enough occurrences per species for subsequent niche calculations. Environmental thinning could not be used here since the distributions of tundra species are naturally biased towards cooler temperatures. The thinned occurrences were further screened using the R-package 'CoordinateCleaner' (2.0-20; Zizka et al., 2019), which flagged 2% of records as potentially problematic (e.g. because of closeness to a botanical institution or being a spatial outlier). Manual check, however, indicated that most of the flagged occurrences were correct, such as sparsely recorded occurrences from Siberia which were flagged as spatial outliers (Figure S3). Thus, we did not remove the flagged occurrences, but accounted for the potential environmental outliers by using only the 95% of occurrences closest
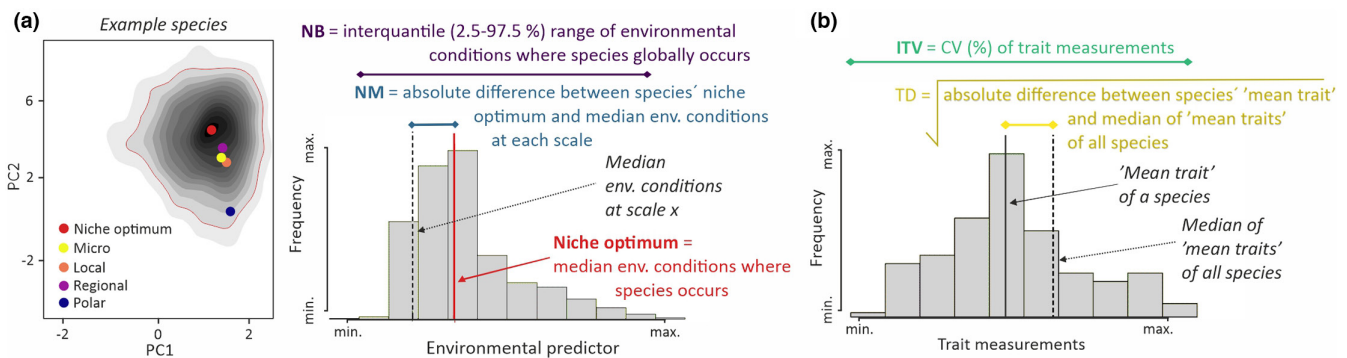
FIGURE 2 Calculation of niche (a) and trait metrics (b) assessed in explaining occupancy of 106 vascular species across the four spatial scales north of Arctic Circle. Niche breadth (NB) and niche marginality (NM) are based on species' global occurrences and environmental factors representing temperature, precipitation, light and soil pH. NB_{PCA} and NM_{PCA} were derived using a two-dimensional kernel density estimation based on the first and second axes of principal component analysis (PCA) of the four environmental factors. NB_{PCA} was defined as the area of the polygon of the 95% kernel density and NM_{PCA} as the Euclidian distance between the centre of the kernel density and the median abiotic conditions of a study area. In addition, niche breadth and marginality were defined per environmental factor based on environmental values of species occurrences. $NB_{Temp.}$, $NB_{Prec.}$, NB_{pH} and NB_{Light} were derived as the interquantile range between 2.5th and 97.5th percentiles, and $NM_{Temp.}$, $NM_{Prec.}$, NM_{pH} and NM_{Light} were derived as the absolute difference between the median and median abiotic conditions of the study area. Intraspecific trait variability (ITV) and trait distinctiveness (TD) are based on trait measurements per species of specific leaf area, plant height and seed mass. ITV was calculated per trait (ITV_{Leaf}, ITV_{Height}, ITV_{Seed}) as coefficient of variation (CV) of measurements and trait distinctiveness per trait (TD_{Leaf}, TD_{Height}, TD_{Seed}) as square root transformed absolute differences between the mean of measurements per species ('mean trait') and median of 'mean traits' of all species. ITV_{SUM} and TD_{SUM} per species were formed by scaling (between 0 and 1 across species) and summing the per trait values.

to niche position in environmental space to derive the niche metrics for each species (see below).

To cover the abiotic constraints of plants (i.e. temperature, moisture, soil and light; Mod, Scherrer, et al., 2016) we used data on MAT (bio1 from CHELSA V1.2; Karger et al., 2017, 2018), annual precipitation sum (bio12 from CHELSA V1.2; Karger et al., 2017, 2018), soil pH (Hengl et al., 2017), and solar radiation (Fick & Hijmans, 2017). These data covered the terrestrial non-glaciated area (excluding Antarctica) and were spatially aggregated to resolution of 30″ (Figure S4). To reduce the environmental dimensions, we performed a principal component analysis (PCA; utilizing the R-package 'RStoolbox' 0.2.6; Leutner et al., 2019) for the four variables. The first and second PC-axes together explained >90% of the data variance (Figure S5). Next, we derived abiotic data (the first and second PC-axis and the original abiotic variables) for each species' thinned global occurrences.

Abiotic niches were defined per species following Broennimann et al. (2012) and Gómez et al. (2016). First, we performed a two-dimensional kernel density estimation for each species using the PCA-values (Figure 2; Figure S6). Next, niche breadth (NB_{PCA}) was derived as the area of the polygon of the 95% kernel density following Broennimann et al. (2012) and Gómez et al. (2016). Niche marginality (NM_{PCA}) was calculated as the Euclidian distance between the centre of the kernel density (i.e. niche position; sensu Tarjuelo et al., 2017) and the median abiotic conditions of a study area following Hirzel et al. (2002). NM values are scale specific, because the median abiotic conditions vary among the study areas (Figure 2; Figures S6 and S7). The visual inspection of the two-dimensional kernel density plots of all species did not indicate that environmental outliers, resulting from possible false occurrence records, would obscure niche metric calculations.

We also calculated the niche metrics per species per abiotic variable (Temp.=temperature, Prec.=precipitation, pH=soil pH, Light=solar radiation). $NB_{Temp.}$, $NB_{Prec.}$, NB_{pH} and NB_{Light} were derived as the interquantile range between 2.5th and 97.5th percentiles of values. $NM_{Temp.}$, $NM_{Prec.}$, NM_{pH} and NM_{Light} were derived as the absolute difference between the median value and median abiotic conditions of the study area (Figure 2).

2.3 | Trait metrics

To derive ITV and TD for the species, we used traits representing leaf–height–seed-scheme, which captures species ability to compete with other species and tolerate stress and disturbances (Westoby, 1998). Measurements of SLA, height and seed mass were derived from three trait databases for the species: TRY a global trait database (Kattge et al., 2011), Tundra Trait Team database (Bjorkman et al., 2018), and Botanical Information and Ecology Network (Maitner et al., 2018). Number of measurements per trait and per species varied from 0 to almost 4500, with median of 34. For the traits and species with less than five measurements, we used data from a coarser taxonomic level as in Niittynen et al. (2020). To

remove faulty entries and other outliers, we removed values exceeding eight standard deviations per species per trait, and then further manually checked the trait measurement distributions to remove unrealistic values.

For ITV, we calculated coefficient of variation (%) of trait measurements per trait (ITV_{Leaf}, ITV_{Height}, ITV_{Seed}; see Figure 2). To have one summary metric (ITV_{SUM}), we scaled (between 0 and 1 across species) and summed ITV_{Leaf}, ITV_{Height} and ITV_{Seed} per species. For TD, we used square root transformed absolute differences between the mean of measurements per species ('mean trait'; see Figure S8) and median of 'mean traits' of all species (TD_{Leaf}, TD_{Height}, TD_{Seed}). For TD_{SUM}, we scaled (between 0 and 1 across species) and summed TD_{Leaf}, TD_{Height} and TD_{Seed} per species. We acknowledge that TD is usually calculated per plot (i.e. species of interest vs. the other species in the plot) and then the plot-specific values are averaged per species (as e.g. in Marino et al., 2020). However, as we had no plot-specific trait measurements across species, we used the median traits of all species to derive TD.

2.4 | Final species selection

At the local scale, 211 species were identified after excluding one hybrid taxa from genus *Salix* and species with ambiguous taxonomy (taxa of *Hierachium* [including *Pilosella* genus] and *Taraxacum* genera and species of *Alchemilla* genus apart from *A. alpina*). For 90 of these species, we could find occurrences at all scales (micro scale being the main limiter) and enough trait measurements. In addition, we also included the species that had the lowest or highest occupancy, NB_{PCA}, NM_{PCA}, ITV_{SUM} or TD_{SUM} among the 211 species at any scale to cover the complete ranges of the metrics (Figures S9 and S10). This resulted in 106 species included in the analyses. Out of these, 70 species have circumpolar distribution, and distribution of only seven species is restricted to Europe (i.e. geographic range spans less than 100° of longitude; Figure S11).

2.5 | Phylogeny

Phylogeny's relatedness to data was assessed, because phylogeny can violate the assumption of the independence of data (Freckleton et al., 2002). The phylogenetic tree for the 106 species was derived from the vascular plant mega-tree (GBOTB.extended) implemented in R-package 'V.PhloMaker' (Jin & Qian, 2019). Phylogenetic relatedness was then assessed against species pairwise differences in occupancy and niche and trait metrics using Mantel test with Spearman correlation. In addition, possible phylogenetic signal was examined by calculating K-statistic using function phylosig (R-package 'phytools' 0.7-80; Revell, 2012). The Mantel correlations were low (−0.09–0.15) and non-significant (except for ITV_{Seed}: $\rho=0.15$; $p=0.001$), and the detected phylogenetic signal was weak (0.004–0.06) for all metrics and statistically significant only for TD_{SUM}, TD_{Leaf} and TD_{Seed} (Table S1). We thus regard phylogeny as

not affecting the results notably (see also Tales et al., 2004) and do not further account for phylogeny in this study.

2.6 | Analyses

Relationships of NB, NM, ITV and TD to occupancy at the four spatial scales were assessed with generalized additive models (GAMs; with spline smoothers from R-package 'mgcv' 1.8; Wood, 2017). The models were fitted with negative binomial distribution to account for overdispersion (Hartig, 2019; Ver Hoef & Boveng, 2007). Smoothing parameters were estimated from the data using option 'REML' (=restricted maximum likelihood) and the default of 10 knots. Higher number of knots did not improve model fit and response curves did not indicate that the number of knots would be too high to result in overfitting. GAMs were chosen as they flexibly allow non-linear responses, which were indicated by preliminary analyses (Table S2).

We assessed the relative and absolute importance of NB, NM, ITV and TD in explaining species occupancy across scales. Relative importance was assessed using multivariate GAMs and variable shuffling (Mod et al., 2021). First, a GAM with all four metrics as predictors was fitted and its R^2 recorded. Then, the model was re-fitted multiple times, but by randomly shuffling one metric at time, and the R^2s of the models were recorded. For each metric, shuffling was done 100 times and the mean decrease in R^2s in comparison

to the original model were calculated. Finally, relative importances were obtained as mean decrease in R^2 per metric proportioned to summed mean decreases of the four metrics. The absolute importances of NB, NM, ITV and TD were assessed as explanatory power of univariate GAMs (measured with R^2).

In addition, the forms of relationships between occupancy and NB, NM, ITV and TD were visualized as response curves following Elith et al. (2005). For this, we used the multivariate GAMS, holding the other metrics than that of interest constant in their median values for predictions.

3 | RESULTS

Occupancy of species varied across the studied four scales, especially between the micro and polar scales (Figure S12). Occupancies between micro and local ($r_s = 0.81$, $p < 0.001$) and between regional and polar scales ($r_s = 0.76$, $p < 0.001$) were strongly and significantly positively correlated. At all scales, occupancy had skewed distribution with tendency towards species with low occupancy. Niche and trait metrics (Figures S13–S20) had weak positive correlations (Figure S21), of which the strongest between NB_{PCA} and ITV_{SUM} ($r_s = 0.35$, $p < 0.001$). Linear relationships between occupancy and niche and trait metrics were in general weak ($r_s < |0.5|$; Table S2; Figure S22).
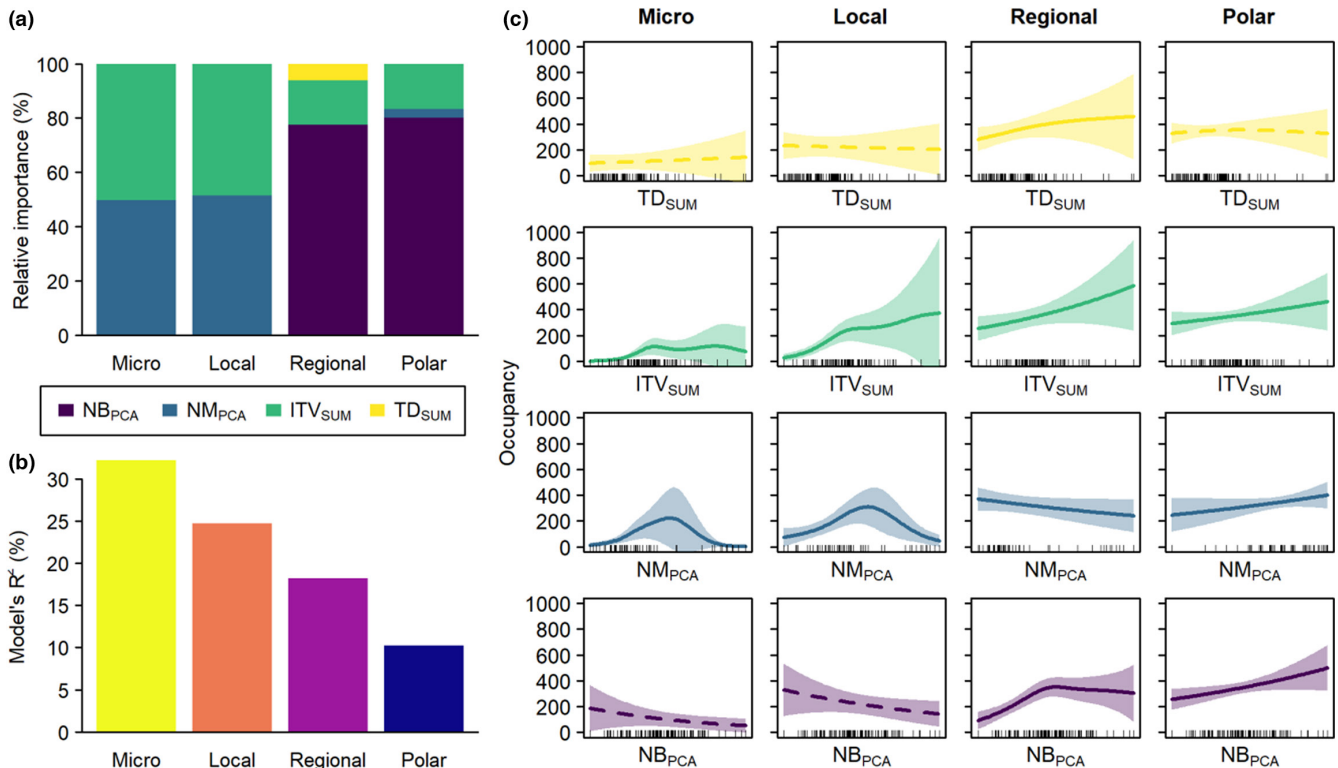
FIGURE 3 Roles of niche breadth (NB_{PCA}), niche marginality (NM_{PCA}), intraspecific trait variability (ITV_{SUM}) and trait distinctiveness (TD_{SUM}) in explaining occupancy of 106 vascular species across the four spatial scales north of Arctic Circle. (a) Relative importance of the predictors. (b) Total variances explained (R^2) by the models. (c) Relationships between occupancy and the predictors. Shaded areas indicate confidence intervals, dashed lines metrics with relative importance of 0% in the model and rugs the distributions of explanatory variables.
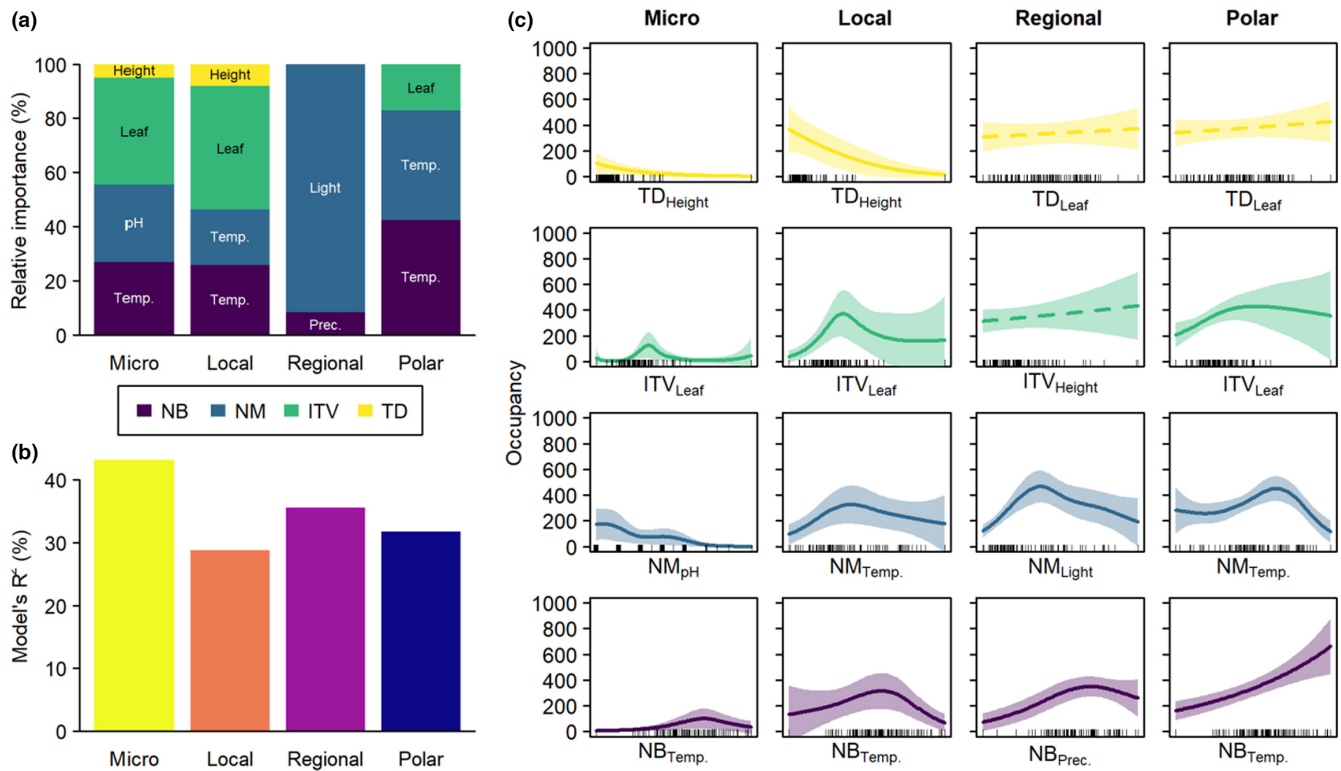
FIGURE 4 Roles of the specific niche breadth (NB), niche marginality (NM), intraspecific trait variability (ITV) and trait distinctiveness (TD) metrics in explaining occupancy of 106 vascular species across the four spatial scales north of Arctic Circle. The predictors were the specific metrics receiving the highest R^2-values in the univariate generalized additive models (Figure S23). (a) Relative importances of the predictors. (b) Total variances explained (R^2) by the models. (c) Relationships between occupancy and the predictors. Shaded areas indicate confidence intervals, dashed lines metrics with relative importance of 0% in the model and rugs the distributions of explanatory variables.

Based on the multivariate GAMs built with NB_{PCA}, NM_{PCA}, ITV_{SUM} and TD_{SUM}, relative importances of the metrics in explaining occupancy varied across the scales (Figure 3). At micro and local scales, NM_{PCA} and ITV_{SUM} mainly explained occupancy's variation, each with relative importance of ~50%. At regional and polar scales, NB_{PCA} and ITV_{SUM} mainly contributed to explain occupancy's variation, with NB_{PCA} explaining relatively more than ITV_{SUM}. Out of the most important metrics, occupancy's response to NB_{PCA} was positive at regional and polar scales, to NM_{PCA} hump-shaped at micro and local scales and to ITV_{SUM} positive at all scales. Total variance explained (i.e. model's R^2) by NB_{PCA}, NM_{PCA}, ITV_{SUM} and TD_{SUM} decreased from micro to polar scale.

The R^2s of univariate GAMs varied across the scales as hypothesised: trait metrics had in general higher R^2 at micro and local scales, whereas niche metrics had in general higher R^2 at regional and polar scales (Figure S23). The univariate GAMs also showed that the niche and trait metrics based on a specific abiotic dimension or trait often better explained occupancy than the summary metric (i.e. NB_{PCA}, NM_{PCA}, ITV_{SUM} or TD_{SUM}).

Rebuilding the multivariate GAMs using the specific metrics of NB, NM, ITV and TD receiving the highest R^2 values in the univariate models continued to support the main hypothesis: At regional and polar scales, niche metrics had higher relative importance than trait metrics in comparison to micro and local scales, where the niche and trait metrics had approximately equal summed relative importance

(Figure 4). The response curves indicated in general positive trends between occupancy and ITV_{Leaf} and $NB_{Temp./Prec.}$, negative trends between occupancy and TD_{Height} (at micro and local scales) and NM_{pH} (micro scale), and hump-shaped trends between occupancy and $NM_{Temp.}$ (local and polar scales) and NM_{Light} (regional scale). The multivariate GAMs fitted with specific metrics showed better model performance across the scales than the models fitted with NB_{PCA}, NM_{PCA}, ITV_{SUM} and TD_{SUM}.

4 | DISCUSSION

In this study, we found that occupancy of species varied across the spatial scales meaning that locally common species can be rare at a broader scale and vice versa (see also Hartley et al., 2004). This variation across scales suggests that the underlying mechanisms of species occupancy might be scale-dependent too (Heino & Tolonen, 2018; Sporbert et al., 2021). Indeed, while both the niche and trait metrics contributed to explaining occupancy at all scales in our study, niche metrics explained variance in species occupancy relatively more at the broader regional and polar scales than at the finer micro and local scales. At the finer spatial scales, the trait metrics were relatively more important than the niche metrics as hypothesised. Given that the used niche metrics should represent

species tolerance and preference of abiotic conditions (Vela Díaz et al., 2020) and traits additionally competitive ability (Kunstler et al., 2016), our findings suggest that abiotic filtering acts more strongly at broader scales than biotic interactions, which are more effective at fine scales within nearby located individuals (Lortie et al., 2004; McGill, 2010).

Consequently, the scale-dependence of the underlying mechanisms should be acknowledged when, for example, anticipating the effects of environmental changes on species occupancy. At a specific site, species' NB covering the change in local abiotic conditions would not be beneficial for occupancy unless the species has traits to compete with the neighbouring and immigrating species. Analogously, a local extinction would pose less of a risk of global extinction for a species with wide NB. Thus, species' responses to alterations in their environment, such as warming climate or invasive species, would be locally more governed by the changes in species community, whereas at the broader scales, tolerance of varying abiotic conditions would be more decisive (Powell et al., 2011; Schweiger & Beierkuhnlein, 2016). Acknowledging the scale-dependencies would also assist in identifying invasive or vulnerable species and choosing the right conservation strategies at the right scales (Hartley & Kunin, 2003; Mack et al., 2007; Magness et al., 2011). However, we note that abiotic and biotic filtering act in concert (e.g. outcomes of biotic interactions being context dependent; Chamberlain et al., 2014; He et al., 2013). Thus, disentangling different mechanisms and forecasting their effects on occupancy is not straightforward.

Our analyses provide two further insights regarding the scale-dependency of importance of niche and trait related metrics in explaining occupancy. First, NB_{PCA} and NM_{PCA} showed evidence of scale-dependency too, and second, a metric based on a specific abiotic dimension or trait often better explained occupancy than the summary metric (e.g. NB_{PCA}, ITV_{SUM}). Regarding the first insight, NB_{PCA} was the more important niche metric at regional and polar scales, whereas NM_{PCA} was the more important at micro and local scales. The likely explanation for this outcome is that the broad extent at regional and polar scales implies large range of abiotic conditions. This, in turn, makes tolerance of varying abiotic conditions (i.e. NB) being the decisive underlying mechanism behind occupancy (Slatyer et al., 2013). The central role of NB in driving occupancy is also supported by a study from French Alps, which albeit the relatively small extent, encompassed large variety of environmental conditions due to elevational differences (Boulangeat et al., 2012). Also in line with our findings, NM's role over that of NB has been identified at finer scale assessments of occupancy when studying trees (Vela Díaz et al., 2020), stream diatoms and insects (Heino & Soininen, 2006; Rocha et al., 2018) and birds (Gregory & Gaston, 2000). Small areas likely contain less variation in habitats and, thus, NM is more important niche metric than NB for occupancy. However, it is to be noted, that in our study, NB was not systematically more important than NM at broader scales and vice versa at finer scales, when assessing the metrics based on a specific abiotic dimension. This could reflect the varying spatial patterns of different environmental factors

(Pickett & Cadenasso, 1995). For example, soil pH shows relatively more variation than macroclimatic conditions across small extents.

The second insight indicates that the roles of niche and traits as underlying mechanisms of occupancy are affected by the abiotic dimensions and traits covered. For example, occupancy at Polar scale was notably better explained by the climate-related niche metrics than NB_{PCA} and NM_{PCA}, likely reflecting the decisive role of macroclimate at broad scales (McGill, 2010). At finer scales, microclimate, soil, snow cover and other factors with fine-scale spatial variation might be more important (Bramer et al., 2018). Thus, identifying the meaningful niche constraints per spatial scale in future studies is essential. At regional scale, the relationship of occupancy was strongest to NM_{Light} with hump-shaped response. Annual amount of solar radiation is primarily determined by latitude, and thus, light optimum also reflects south–north niche position of species. As most studied species have higher light optima than the median annual solar radiation at regional scale (Figure S7), the non-marginal (i.e. species with low NM_{Light}) and marginal species (i.e. high NM_{Light}) represent "northern" and "southern" species, respectively. Whereas NM itself could limit occupancy of the southern species (Murphy et al., 2006), northern species could be rare due to harsh conditions and limited resources restricting plant growth (Ives & Barry, 2019). This leaves the species with average NM_{Light} having the highest occupancy. Thus, the hump-shaped relationship of NM_{Light} at regional scale would not represent species preference of solar radiation per se but a combination of NM and abiotic filtering. Low occupancy of "northern" species could also be affected by sampling bias towards warmed conditions and "southern" species, if the environmental filtering did not sufficiently balance the bias. Among the traits, ITV_{Leaf} and TD_{Height} better explained occupancy than ITV_{SUM} or TD_{SUM}, respectively. Evidence for the choice of traits affecting importance of trait metrics in explaining occupancy exists in the study from a grassland ecosystem by Bergholz et al. (2021). However, their finding of ITV_{Height} being more important than ITV_{Leaf} is opposite to ours. Reason for the varying results could be the different study ecosystems. At grasslands, ability to adapt plant height might be important in light competition, whereas in cold and nutrient-poor arctic environment, ability to adapt SLA, which is related to resource competition, could be more important (Kemppinen et al., 2021; Lauterbach et al., 2013).

While we were primarily interested in the relative roles of niche and trait metrics across scales, our analyses also allow to inspect the forms of relationships between occupancy and the niche and trait metrics. These were mainly as anticipated, especially for ITV, yet, instead of simple linearity, some response curves of GAMs indicated curvilinear relationships, reflected also in low correlations (Table S2). For example, the species with the largest NBs were not those with the highest occupancy at the finest scales (i.e. the relationships were hump-shaped or even negative). This could be explained by the trade-off between stress-tolerance and competitive ability (Chase & Leibold, 2003). At finer scales, with less abiotic heterogeneity and more competition, it would not be beneficial to have large NB with the cost of lower competitive ability.

NM, when explaining occupancy, had mostly a hump-shaped relationship instead of the assumed negative trend found in former research (Heino & Grönroos, 2014; Vela Díaz et al., 2020; e.g. Venier & Fahrig, 1996). The hump-shaped relationship means that in addition to the species with low habitat availability, also the species favouring the average abiotic conditions, were rare. In addition to the reasoning regarding the NM_{Light} at regional scale, this could be due to most species favouring the environmentally average habitats (Figure S10) which leads to competition, which in turn then decrease occupancies (Bertness & Callaway, 1994). Finally, TD played minor role in our study, which could result from the fact that we could not derive this metric using trait variations within local communities as for example in Marino et al. (2020). The responses to TD were in addition against what was hypothesised. At regional scale, the response to TD_{SUM} was slightly positive, meaning that distinctive traits would be beneficial for occupancy. However, instead of an indication of competitive ability, this may be a result of distinctive traits making a species easier to detect (Chen et al., 2013). At the two finer scales the response to TD_{Height} was negative, meaning that the species close to the average height of all species (here short; see Figure S8) had higher occupancy. This likely reflects the dominating stress-tolerant life-strategies (Grime, 1977; Westoby, 1998) in the Arctic where smaller species better cope with the harsh environment (Bliss, 1962). Therefore, in tundra environment at a fine scale, plant height might better represent the adaptation to abiotic conditions than competitive ability (cf. height's role in light competition e.g. in dry grasslands; Lauterbach et al., 2013).

It should also be noted that even at their best, our models could explain maximum ~40% of variance in occupancy. This likely reflects omission of the stochastic mechanisms, such as dispersal and ecological drift (Vellend, 2010), and influential environmental dimensions and traits at some scales, such as glaciation history, microclimate and life-history (Marino et al., 2020). For example, species ability to disperse could affect occupancy (McGeoch & Gaston, 2002). However, seed mass (Ehrlén & Eriksson, 2000; under the assumption smaller and lighter seeds can disperse further; Westoby et al., 1996) had negligible explanatory power at any scale in our preliminary test (results not shown). Instead of ruling out the role of dispersal ability, this more likely implies that dispersal ability consists also of other factors than seed mass, such as adhesive structures and recruitment ability (Kiviniemi & Eriksson, 1999). Thus, the roles of dispersal ability and other mechanisms in explaining occupancy across scales remain to be assessed in future studies.

Further, all our analyses, results and interpretations are based on the plausibility and ecological soundness of the data and the metrics. While we carefully aimed to derive and prepare data so that the metrics represent the intended mechanisms and so that we could tease apart the sole effect of spatial scale, issues remain that can weaken our findings. First, to study the same set of species across scales limited the species to those found at the finest scales. The studied 106 species represent only a fraction of the species occurring north of the Arctic Circle (>2000 species according to GBIF) and are biased to more common species (Figure S24). If ecology or physiology of these 106 species vary—due to, e.g., biogeographic history (Liebergesell et al., 2016) or boreal influence in Fennoscandia (Ahti et al., 1968; Virtanen et al., 2016)—from all tundra species, our results might not be generalizable to whole of Arctic. Also, while phylogeny of these 106 species should not influence the derived results, low evidence of phylogenetic signal was observed.

Second, the reliability of occupancy and niche metric values are dependent of representativeness of occurrence data. Inventory data, as used in micro and local scales, would be more appropriate to determine species occupancy than spatially, environmentally and taxonomically biased opportunistic data. However, systematic inventory data are rarely available for large extents. Thus, while we aimed to reduce the bias, occupancies at regional and polar scales and niche metrics are underestimates for species that are tricky to detect (Chen et al., 2013) or are not in equilibrium with their environment (Araújo & Pearson, 2005). For example, low Arctic plant diversity suggests that species still migrate northward since the last deglaciation (Stewart et al., 2016).

Third, the niche metrics are assumed to represent the abiotic conditions where a species can persist and maintain stable population (i.e. fundamental niche; Hutchinson, 1957). However, an occurrence does not necessarily mean a viable population and occupancy is also constrained by dispersal and biotic interactions. Thus, the niche metrics based on observed natural occurrences might not represent fundamental niches (Jiménez et al., 2019; Lee-Yaw et al., 2022). Similarly, metrics based on measured traits do not directly contain information of species competitive ability but are used as an indication of it under the assumption that higher ITV and TD are useful in competition.

Fourth, global data to derive niche and trait metrics avoid niche truncation and cover whole trait variation, but assumes spatial niche conservatism (Wasof et al., 2015; Wiens et al., 2010) and omits local adaptations (Leimu & Fischer, 2008). If niches and traits vary among populations and regions (Vieira et al., 2021), relationships between fine scale occupancy and local niche and trait metrics might deviate from what we found here. In addition, the occurrences to calculate occupancy at polar scale and niche metrics are partly the same (especially if species' geographic range is limited to Arctic) which might lead to the relationships between occupancy and niche metrics partly stemming from spatial autocorrelation (Cardillo et al., 2019; Ficetola et al., 2020). Similarly, positive relationship between occupancy and ITV may partly stem from circularity since common species tend to have also more trait measurements, possibly leading to higher variance. However, the correlations between coefficients of variation and numbers of trait measurements were weak and significant only for ITV_{Leaf} (Figure S25).

Finally, we recognize that species occupancy is rarely studied alone as a strong tradition exists to examine it together with abundance and trying to unravel the mechanisms behind the positive relationship between the two (Borregaard & Rahbek, 2010; Gaston et al., 2000) or to examine occupancy as one of the many dimensions of rarity (Rabinowitz, 1981). Here, we chose to concentrate only on occupancy because deriving abundance data across scales in harmonized manner was not possible. However, we acknowledge the value of future studies of scale-dependency where

abundance or other dimensions of rarity would be incorporated (He & Gaston, 2000). Further, here the broader scales were produced by simultaneously increasing the extent and decreasing the resolution. Such relationship of the two fundamental components of spatial scale is typical, yet it makes it impossible to assess whether the observed scale-dependencies in underlying mechanisms of occupancy are due to differences in extent, resolution or both (Sandel, 2015).

In this study from tundra environments with 106 vascular plant species, we found that relationships between species occupancy and NB, NM, intraspecific trait variation and TD are scale-dependent. At the finer scales, metrics related to the species traits better explained occupancy than at broader scales, where niche metrics, in turn, had relatively stronger explanatory power. Under the assumption that the used niche metrics represent tolerance and preference of abiotic conditions whereas traits in addition can indicate species' competitive ability, our results from Arctic study areas are in line with general assumption of abiotic filtering acting at broader scale than biotic interactions. From an applied point of view, our findings highlight that spatial scale should be acknowledged when planning conservation of rare species and biodiversity and when assessing species susceptibility to environmental change and invasions.

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CONFLICT OF INTEREST STATEMENT

The authors of this manuscript declare that there is no conflict of interest and that funders had no role in the planning, implementing or reporting the study.

DATA AVAILABILITY STATEMENT

Occupancy and niche and trait metrics at all scales used in this study are provided as an Appendix. Species occurrence data to calculated species occupancies at micro, local, regional and polar scales are further stored in Dryad: https://doi.org/10.5061/dryad.76hdr7t1r.

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BIOSKETCHES

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SUPPORTING INFORMATION

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