Multiple Spatial Scale Analysis of the Niche Characteristics of the *Rhododendron dauricum* Plant Communities in Northeast China

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Abstract: This study aims to verify the concept of niches at multiple spatial scales in plant communities. To this end, we analyzed the niche characteristic of *Rhododendron dauricum* plant communities in Northeast China at three spatial scales. At the local scale, we calculated the Importance Value (*IV*) of species in five communities in the north of the Da Hinggan Mountains. At the intermediate scale, we examined five communities in their entirety, calculated the niche breadth of the species, and integrated niche overlap and interspecific association to analyze interspecific relationships. Further, the generalized additive model (GAM) was used to analyze the impact of topography and soil factors on niche characteristics. At the regional scale, we analyzed the geographical distribution of dominant species of *R. dauricum* plant communities in Northeast China and used principal component analysis (PCA) to analyze the impact of geographical and climate factors on species distribution. The results show that at the local scale, the *IV* of the species in each community varies widely. At the intermediate scale, species with a wide niche breadth tend to have a high value for *IV*. *Larix gmelinii*, *Betula platyphylla*, *R. dauricum*, *Ledum palustre*, and *Vaccinium vitis-idaea* had a relatively wide niche breadth and a high niche overlap, and the interspecific associations were almost all positive. Elevation and soil nutrients were the most dominant environmental factors. At the regional scale, species with a wide niche breadth tend to have a wide range of distribution, and temperature and precipitation were the most dominant environmental factors. This study suggests that the niche characteristics at three scales are both related and different. Niche characteristics at the local scale were various and labile, and niche characteristics at the intermediate and regional scales were relatively regular. These results show some degree of consistency with previous studies from an evolutionary perspective. The action mechanisms of these communities are related to differences in the dominant environmental factors. In addition, the integration of niche overlap and interspecific association determine interspecific relationships more accurately.

Keywords: niche; spatial scale; *Rhododendron dauricum*; niche breadth; niche overlap; interspecific association; environmental factor

1 Introduction

In ecological studies, study scale has always been a key issue to be considered (Liang et al., 2011b; Estes et al., 2018), and niches are no exception. Silvertown et al. (2006a) proposed three niche concepts at a hierarchy of spatial scales and analyzed their characteristics from an evolutionary perspective. Specifically, the niche at the local scale is named the *α* niche, which emphasizes the interactions of species; this scale is generally within the plant community. The niche at the intermediate scale is named the *β* niche, which is equivalent to the 'habitat

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niche' and emphasizes the environmental gradients; this niche's scale is generally between different communities. The niche at the regional scale is named the *γ* niche, which emphasizes geographic distribution, and its scale is generally an entire region (Silvertown et al., 2006a; Geange et al., 2011). In evolution, the *α* niche is labile, the *β* niche is conservative, and the *γ* niche is related to geographic distribution, which may also be conservative (Silvertown et al., 2006a; 2006b). However, these concepts are rarely verified in plant communities. Most previous studies focused on only one or two scales—for instance, studies of temperate grazing land communities at the local and intermediate scales, submerged aquatic vegetation communities at the regional scale, and, even larger, invasive plants at the intercontinental scale (Anthwal et al., 2008; Treier et al., 2009; Kotta et al., 2014). Therefore, niche studies of multiple scales remain incomplete, especially for temperate forest communities. At present, the niche characteristics of plant communities have not been comprehensively and systematically studied from multiple scales (local, intermediate, and regional), and their mechanisms of action have not been explored. Furthermore, niches of plant species tend to be closely related to environmental factors, and multiple spatial scales will inevitably lead to a variety of environmental gradients (Lamanna et al., 2014; Schellenberger Costa et al., 2018). Thus, niche characteristics at different scales may be affected by environmental factors.

In niche studies, niche breadth and overlap are two important concepts for niche metrics, but they both have some limitations. For niche breadth, one limitation is the difficulty in producing accurate estimations, especially for plant species. On the one hand, multifarious resources are necessary for plant survival, growth, and fecundity. Furthermore, the habitat of a plant integrates entities from various environment elements. Therefore, it is unrealistic to analyze every resource dimension occupied by plants separately (Marinšek et al., 2015). On the other hand, the necessary resources of most plants are common—for example, light, water, CO_2, and soil nutrients. Consequently, it is not enough to simply consider the resource dimension; one must also consider the resource utilization mode and time dimension (Silvertown, 2004). Estimating species responses along specific dimensions is preferable to analyzing the filtering and limiting effects of specific environmental factors.

Instead, defining a comprehensive resource state (usually represented by quadrats) is better able to embody the total resources dimension and position and function of a plant in a community. Niche overlap is often used to analyze interspecific relationships. Nevertheless, this overlap is not always positively correlated with the intensity of the competition between two plant species. On the contrary, a strong niche overlap leads to facilitation in some plant communities (i.e., the stress gradient hypothesis, SGH) (Fajardo and McIntire, 2011). In this regard, the correlation between niche overlap and interspecific relationships needs more concrete analyses. Except for niche overlap, interspecific association can also reveal interspecific relationships and help to discern the process of community assembly and the tendency of community succession (Gotelli and McCabe, 2002; Sfenthourakis et al., 2006; Tatsumi et al., 2018). In previous studies, due to the spatial character of interspecific association, niche overlap was invariably associated with spatial pattern analysis (Nguyen et al., 2016), and the study objects for the integration of niche overlap and species association were mostly animals (Pinheiro et al., 2011; Ratcliffe et al., 2014). However, the biological mechanisms of plant community spatial clumping and segregation tend to be explained by the concept of a niche (Adler et al., 2010; Wang et al., 2010). Hence, the integration of niche overlap and interspecific association may be a relatively robust way to reveal interspecific relationships.

The ecological study of temperate forests usually focuses on trees but pays less attention to shrubs (Murphy et al., 2015; Piedallu et al., 2016). *Rhododendron dauricum* is a vital component of the temperate forest shrub layer and is widely distributed in Northeast China. Moreover, *Larix gmelinii-R. dauricum* forest is one of the main forest types in Northeast China, especially in the Da Hinggan Mountains (Jiang et al., 2016; Zhang et al., 2018). *R. dauricum*'s medicinal value and artificial cultivation are the focus of most current research, but ecological issues are less commonly studied (Mittal et al., 2012; Saeki et al., 2018). As one of the most important ecological issues, a niche can not only reveal interspecific relationships and community stability but can also serve as one of the core mechanisms of community assembly (Tanentzap et al., 2015; Bulleri et al., 2016; Gainsbury and Meiri, 2017; Niklaus et al., 2017). Thus, niche studies can reveal the compositions, interactions,

functions, and statuses of species in *R. dauricum* plant communities. In brief, our overall goal is the verification of niche characteristics at the local, intermediate, and regional scales with *R. dauricum* plant communities in Northeast China. Further, we analyzed the impact of environmental factors on niche characteristics and integrated niche overlap and interspecific association to determineinter specific relationships. It should be emphasized that we only analyzed the features of niche characteristics at three scales, rather than comparing them in parallel, and did not completely extend the results of one scale to another.

2   Materials and Methods

2.1   Study area

The study area at the local and intermediate scales was Huzhong District (51º14′40″N–52º25′00″N, 122º39′30″E–124º21′00″E) (Fig. 1), which is located in the north of the Da Hinggan Mountains, with a total area about 7.420 × 10³ km² (Li et al., 2014). This district is located in a cold temperate zone and features a continental monsoon climate. The mean annual precipitation is 497.7 mm/yr, and the annual meantemperature is −4.3℃. The most representative soil type is brown coniferous forest soil. The zonal vegetation type is a cold temperate coniferous forest. The tree layer is mainly composed of *L. gmelinii*, *Pinus sylvestris*, *Picea koraiensis*, *Betula platyphylla*, *Populus davidiana*, and *Chosenia arbutifolia*; the shrub layer is mainly composed of *Pinus pumila*, *R. dauricum*, *Ledum palustre*, and *Vaccinium vitis-idaea*; and the herb layer is mainly composed of *Deyeuxia angustifolia*, *Carex*, and *Vicia* (Chen et al.,

2011). In addition, the names of the plant taxa cited in this study are based on the Flora of China database (http://foc.iplant.cn/).

The study area at the regional scale included Northeast China. This area is located in the northeastern area of China (38º43′N–53º34′N, 115º31′E–133º05′E), with a total area of about 1.236 × 10⁶ km². The geomorphic characteristics of Northeast China are as follows: 'high in three sides and low in the middle'—The Da Hinggan Mountains, Xiao Hinggan Mountains, and Changbai Mountains are in the western, northern, and eastern areas, respectively. Most of the region features a temperate monsoon climate, and part of the area is under a temperate continental climate in the west. The mean annual precipitation ranges from 174 to 1124 mm/yr, and the annual mean temperature ranges from −8.8 to 11.3℃ (from east to west, the precipitation decreases; from south to north, the temperature drops). Due to the influence of many factors, such as latitude, climate, and the location of land and sea, there are three precipitation region from east to west: a humid region (annual precipitation > 800 mm), a semi-humid region (400–800 mm), and a semi-arid region (200–400 mm) (Liang et al., 2011b). Consequently, the vegetation types of this region have obvious meridional zonality and transitional characteristics: from east to west, there is temperate deciduous broad-leaved forest, cold temperate deciduous coniferous forest, and temperate grassland (Zhang et al., 2011). Temperate deciduous broad-leaved forest areas include mixed broadleaf-conifer forestand deciduous broad-leaved forest. Mixed broadleaf-conifer forest is mainly distributed in the Xiao Hinggan Mountains and Changbai Mountains, whose dominant species are *Pinus*
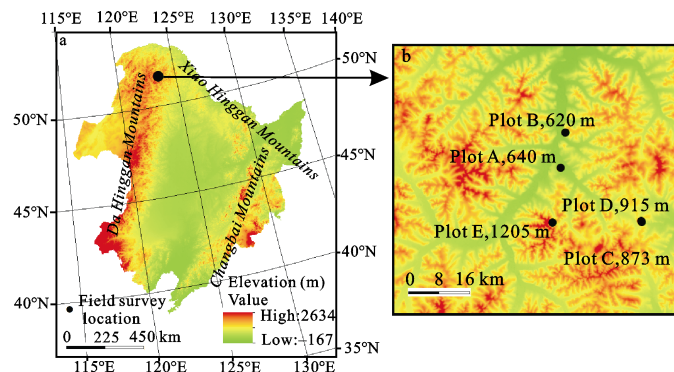

Fig. 1   Location of study area and field survey plots. a. Northeast of China; b. Five field survey plots selected in Huzhong District based on three elevation gradients (600 m, 900 m, and 1200 m). The longitude and latitude of plot C and plot D are close, but the slope position and aspect are different

koraiensis, *Picea asperata*, and *Quercus mongolica*. Deciduous broad-leaved forest is mainly distributed in the Liaodong Peninsula and western Liaoning Mountains, whose dominant species are *Pinus densiflora*, *Pinus tabuliformis*, and *Quercus*. Cold temperate deciduous coniferous forest is mainly distributed to the north of the Da Hinggan Mountains, whose dominant species are *L. gmelinii* and *P. sylvestris*. Temperate grassland is mainly distributed in the Songliao Plain, north of the Da Hinggan Mountains and to the east of Inner Mongolia, whose dominant species are *B. platyphylla*, *Q. mongolica*, *Leymus chinensis*, and *Stipa* (Xu et al., 2008).

2.2 Data collection and analysis methods at the local scale

Based on three elevation gradients (600 m, 900 m, and 1200 m), five field survey plots were selected in Huzhong District (Table 1). The lengths and widths of the plots were both 60 m (60 m × 60 m), and every plot was divided into 36 tree quadrats (10 m × 10 m) and 144 shrub quadrats (5 m × 5 m). In addition, 40 herb quadrats (1 m × 1 m) were randomly selected in each plot. In total, the area of each plot was 1.8 ha, the number of tree quadrats was 180, of shrub quadrat was 720, and of the herb quadrat was 200. We performed a forest community survey from May to August in 2018. Specifically, for each tree quadrat, the species name, number,

height, coverage, crown breadth, and breast diameters of the trees were measured and recorded. In each shrub and herb quadrat, the species name, number, height, and coverage of shrubs and herbs were measured and recorded. At the local scale, five plots were regarded as five mutually independent plant communities with various site conditions. We used the Importance Value (*IV*) (Chai et al., 2012, Equation (1)) of the species in each community to represent the niche characteristics of the species at a local scale. *IV* is a comprehensive index used to measure the status and function of one species in the community (Arroyo-Rodríguez and Mandujano, 2006). In addition, it is the basic value for calculating niche breadth and overlap.

$$IV = (x + y + z)/3 \tag{1}$$

Where x is the relative abundance, y is the relative frequency, and z is the relative dominance.

2.3 Data collection and analysis methods at the intermediate scale

In each shrub quadrat, the elevation, aspect, and slope were measured by hand-GPS and a geologic compass. The soil temperature, moisture, and pH were measured by a soil temperature and moisture recorder (TZS-2X-G, China Tuopuyunnong) and a soil pH tester (TZS-pH-IG, China Tuopuyunnong); soil of 0–20 cm thickness was sampled to measure it selement contents. The total carbon

Table 1 Characteristics of the five field survey plots in Huzhong District

Content	Plot A	Plot B	Plot C	Plot D	Plot E
Longitude	123°34′37.49″E	123°35′33.49″E	123°50′41.46″E	E123°50′34.70″	123°32′54.44″E
Latitude	51°43′55.87″N	51°48′17.12″N	51°37′07.63″N	N51°37′15.12″	51°37′10.68″N
Elevation (m)	640	620	873	915	1205
Terrain	Mountain land	Mountain land	Mountain land	Mountain land	Mountain land
Aspect	Northeast	West	Southeast	Southwest	South
Slope (°)	5	20	10	10	15
Slope position	Lower	Middle lower	Lower	Top	Middle upper
Forest origin	Secondary forest	Secondary forest	Secondary forest	Secondary forest	Virgin forest
Forest type	*Larix gmelinii* forest	*Larix gmelinii, Betula platyphylla and Populus davidiana* forest	*Betula platyphylla* forest	*Betula platyphylla* forest	*Larix gmelinii* forest
Canopy density (%)	60	50	55	45	40
Soil type	Brown coniferous forest soil	Peat mire soil	Brown coniferous forest soil	Brown coniferous forest soil	Brown coniferous forest soil
Thickness of litter layer (cm)	8	5	15	10	8
Soil pH	5.7	5.4	5.6	5.5	5.2

(TC) and nitrogen (TN) content was determined by an elemental analyzer (vario MACRO cube, Germany Elementar), the total phosphorus (TP) content was determined by an ultraviolet spectrophotometer (UV-1800, Japan Shimadzu), and the total potassium (TK) content was determined by an atomic absorption spectrometer (Analyst 800, USA PE). The data for the tree quadrat was the average of four shrub quadrats.

At the intermediate scale, we took five communities as the entirety and used the Levins niche breadth (B_1) (Equation (2)) and Hurlbert niche breadth (B_2) (Equation (4)) to represent the niche characteristics of the species. B_1 treats all resource states equally and indiscriminately, while B_2 takes into account the capacity of a population to utilize resources and adapt to ecological factors (Levins, 1968; Hurlbert, 1978).

$$B_1 = -\sum_{j=1}^{r} \left(P_{ij} \log P_{ij} \right) \tag{2}$$

$$P_{ij} = n_{ij} \Big/ \sum_{j=1}^{r} n_{ij} \tag{3}$$

$$B_2 = (B_n - 1) / (r - 1) \tag{4}$$

where P_{ij} is the frequency of the utilization of resource j by specie i for all resources, n_{ij} is the dominance of specie i for resource j (represented by the IV of the species in quadrats), r is the number of resource levels (represented by the number of quadrats), and B_n is the transition value, $B_n = 1 \Big/ \sum_{j=1}^{r} \left(P_{ij} \right)^2$. B_1 has a range of [0, log$r$], and B_2 has a range of [0, 1].

Niche overlap refers to a situation in which two species utilize the same level of resources and overlap each other in a certain resource sequence. In this study, the niche overlap index (O_{ik}, Pianka' formula) (Equation (5)) and curve average model (C_{ih}, Schoener' formula) (Equation (6)) were used to represent niche overlap in the community. O_{ik} objectively reflects the similarity of resource utilization or ecological adaptation among populations and has strong biological significance. C_{ih}'s advantages are its simplicity intrans forming discrete data to continuous data and its strong geometric significance (Pianka, 1973; Thompson et al., 1999; Mouillot et al., 2005). To ensure the conciseness of the results, we only analyzed the dominant species of the tree and shrub layers.

$$O_{ik} = \sum_{j=1}^{r} P_{ij} P_{kj} \Big/ \sum_{j=1}^{r} \left(P_{ij} \right)^2 \tag{5}$$

$$C_{ih} = 1 - \frac{1}{2} \sum_{j=1}^{r} \left| P_{ij} - P_{hj} \right| \tag{6}$$

where P_{ij}, P_{kj} and P_{hj} are the frequency of the utilization of resource j by specie i, specie k, and specie h for all resources, respectively, and their calculation formula are the same as Equation (3), and r is the number of resource levels (represented by the number of quadrats). O_{ik} and C_{ih} both have a range of [0, 1].

Interspecific association refers to the interrelation of different species in spatial distribution, and we used the variance ratio (VR) (Equation (9)) to test the degree of overall association between species in the communities of the sample plots (Pielou, 1974; Schluter, 1984; Su et al., 2015; Yang et al., 2016). Based on the area of the tree and shrub quadrat, the interspecific association was analyzed at 10 m × 10 m and 5 m × 5 m scales.

$$\delta_r^2 = \sum_{i=1}^{s} \left[\frac{n_i}{N} \left(1 - \frac{n_i}{N} \right) \right] \tag{7}$$

$$S_r^2 = \frac{1}{N} \sum_{j=1}^{N} \left(T_j - t \right)^2 \tag{8}$$

$$VR = S_r^2 \Big/ \delta_r^2 \tag{9}$$

where δ_r^2 is the total sample variance, S is the total number of species, N is the total number of quadrats, n_i is the number of quadrats in which specie i appears, S_r^2 is the total species variance, T_j is the total number of species that appear in quadrat j, t is the average of number of species in all quadrats, and $t = (T_1 + T_2 + \ldots + T_n) / N$. When $VR > 1$, the spatial distribution of species is positively correlated. When $VR < 1$, the spatial distribution of species is negatively correlated. When $VR = 1$, the spatial distribution of species has no correlation. In addition, we used the statistical magnitude (W) to test the significance, $W = VR \times N$. When the W value falls within 90% of the confidence interval of the chi-square distribution ($x_{0.95}^2 (N) < W < x_{0.05}^2 (N)$), the correlation of species is insignificant; otherwise, it is significant.

The association coefficient (AC) (Equations 10–12) was used to measure the interspecific association inten-

sity of two species.

$$AC = (ad - bc)/((a+b)(b+d))(ad \geq bc) \qquad (10)$$

$$AC = (ad - bc)/((a+b)(a+c))(bc > ad, d \geq a) \quad (11)$$

$$AC = (ad - bc)/((b+d)(c+d))(bc > ad, d < a) \quad (12)$$

where *a* is the number of quadrats in which two species both appear, *b* and *c* are the number of quadrats in which only one species appears, and *d* is the number of quadrats in which two species both do not appear. Formula *AC* has a range of [−1, 1]; the closer the *AC* value is to 1, the stronger the positive correlation between the species. The closer the *AC* value is to −1, the stronger the negative correlation between the species. If the *AC* value is 0, the two species are completely independent.

The interspecific association significance was tested by a chi-square (x^2) (Equation (13)) test with Yates' continuous correction formula, as follows:

$$\chi^2 = N\left(\left|ad - bc\right| - \frac{1}{2}N\right)^2 \Big/ ((a+b)(b+d)(c+d)(a+c)) \qquad (13)$$

where *N, a, b, c,* and *d* are the same as above. If $6.635 > x^2 > 3.841$, the correlation of the two species is significant ($P < 0.05$). If $x^2 > 6.635$, the correlation of the two species is extremely significant ($P < 0.01$).

In addition, the generalized additive model (GAM) was used to analyze the responses of niche characteristics along with the environmental gradients (Song et al., 2013). The principle of GAM is a regression analysis, which considers that plant species data indicate the responses of environmental variables (Zhu and Kang, 2005). The advantage of GAM is that it can accommodate more models (the relationships between plant species and environmental variables) and has a better fit to the original data. In addition, GAM can automatically select the appropriate polynomial without estimating the regression parameters. In GAM, the environmental variables and plant species data are defined as a relevant variable and an explanatory variable, respectively. There can be more than one relevant variable, but only one explanatory variable. The explanatory variableis is generally the value of dominance of the plant species in the community. In this study, ten environmental factors were taken as the relevant variable, including elevation, aspect, slope, soil temperature, moisture, pH, TC, TN, TP, and TK; the *IV* of

the species in the quadrats was used as the explanatory variable. The package 'mgcv' was employed to run the GAM analysis in the statistical R software.

2.4 Data collection and analysis methods at the regional scale

At the regional scale, the dominant species in the tree and shrub layers of *R. dauricum* plant communities were selected as the study objects. The data of species distribution in Northeast China was taken from the Northeast Biological Herbarium (http://ifp-cas.cn) and the Northeastern Forest Plant Germplasm and Habitat Survey Data Sharing Platform (http://cnes.iae.ac.cn). The environmental data for Northeast China include topography, climate, soil, and vegetation data, for a total of 30 (Table 2). Topography data were taken from the Geospatial Data Cloud (http://www.gscloud.cn), the climate data were taken from WorldClim (http://worldclim.org), soil data were taken from WestDC (http://westdc.westgis.ac.cn), and vegetation data were acquired from Resource and Environment Data Cloud Platform (http://www.resdc. cn). All environmental data were extracted and calculated by ArcGIS 10.3 (ESRI, USA) with a 30 arc-second spatial resolution. Based on ArcGIS, we used the 'Extraction' tool from the 'Spatial Analyst Tools' to extract the environmental data. The extraction method used 'Extract Values to Points'. Moreover, the input point features were the distribution data (longitude and latitude) of the plant species, and the input raster was the environmental data. We used ArcGIS 10.3 to illustrate the geographical distribution of species. The elevation map of Northeast China was used as the background layer, and the distribution data for plant species were added. As a multivariate statistical method for environmental factors, principal component analysis (PCA) transforms multiple data into a few uncorrelated comprehensive indexes by reducing the dimensions of high-dimensional data. PCA simplifies data and obtains the weight of each individual datum, which makes it easier to reveal the characteristics and rules of the data. In this study, PCA was used in SPSS 23 to select the main environmental factors limiting the distribution of the dominant species.

3 Results

3.1 Niche characteristics at the local scale

In the five communities, the species with a high *IV* were different (Table 3). A species' *IV* was also different in

Table 2   Environmental factors of the regional scale (Northeast China).

Category	Data source	Variables	Description	Units
Topography	Geospatial Data Cloud	ELE	Elevation	m
		ASP	Aspect	°
		SLO	Slope	°
Climate	WorldClim	Bio 1	Annual mean temperature	℃
		Bio 2	Mean diurnal range (mean of monthly (max temp – min temp))	℃
		Bio 3	Isothermality (diurnal range/ annual range)	
		Bio 4	Temperature seasonality (standard deviation ×100)	℃
		Bio 5	Max temperature of warmest month	℃
		Bio 6	Min temperature of coldest month	℃
		Bio 7	Temperature annual range	℃
		Bio 8	Mean temperature of wettest quarter	℃
		Bio 9	Mean temperature of driest quarter	℃
		Bio 10	Mean temperature of warmest quarter	℃
		Bio 11	Mean temperature of coldest quarter	℃
		Bio 12	Annual precipitation	mm
		Bio 13	Precipitation of wettest month	mm
		Bio 14	Precipitation of driest month	mm
		Bio 15	Precipitation seasonality (standard deviation ×100)	mm
		Bio 16	Precipitation of wettest quarter	mm
		Bio 17	Precipitation of driest quarter	mm
		Bio 18	Precipitation of warmest quarter	mm
		Bio 19	Precipitation of coldest quarter	mm
Soil	WestDC	GRA	Gravel content	%
		SAND	Sand content	%
		SILT	Silt content	%
		CLAY	Clay content	%
		OC	Organic carbon content	%
		PH	pH	
		ST	Soil type	
Vegetation	Resource and Environment Data Cloud Platform	VT	Vegetation type	

different communities. According to the dominant species in the tree layer, these communities can be classified into three forest types: *L. gmelinii* forest (plot A and plot E), *L. gmelinii*, *B. platyphylla,* and *P. davidiana* forest (plot B), and *B. platyphylla* forest (plot C and plot D). Accordingly, within plot A, in the tree layer, the dominant species was *L. gmelinii*, accompanied by a small amount of *B. platyphylla* and rare *P. davidiana*; in the shrub layer, the dominant species were *R. dauricum*, *L. palustre,* and *V. vitis-idaea*; in the herb layer, the dominant species was *Pyrola incarnate*. Within plot B, in the tree layer, the dominant species were *L. gmelinii*, *B. platyphylla,* and *P. davidiana*; in the shrub layer, the dominant species were *R. dauricum*, *L. palustre,* and *V. vitis-idaea*; in the herb layer, the dominant species was *D. angustifolia*. Within plot C, in the tree layer, the dominant species was *B.*

platyphylla, accompanied by a small amount of *L. gmelinii*; in the shrub layer, the dominant species were *R. dauricum* and *V. vitis-idaea*; in the herb layer, the dominant species was *D. angustifolia*. Within plot D, in the tree layer, the dominant species was *B. platyphylla*, accompanied by a small amount of *L gmelinii*; in the shrub layer, the dominant species were *R. dauricum*, *L. palustre*, and *V. vitis-idaea*; in the herb layer, the dominant species was *D. angustifolia*. Within plot E, in the tree layer, the dominant species was *L. gmelinii*, accompanied by a small amount of *B. platyphylla*; in the shrub layer, the dominant species were *P. pumila* and *V. vitis-idaea*; in the herb layer, the dominant species were *Saxifra gabronchialis* and *Dryopteris fragrans*. Thus, the niche characteristics at the local scale were various and labile.

Table 3 Importance value (*IV*) of the dominant species in *Rhododendron dauricum* plant communities at the local scale

Layer	Species	Plot A	Plot B	Plot C	Plot D	Plot E
Tree layer	*Larix gmelinii*	29.505	9.559	10.807	11.606	23.508
	Pinus sylvestris		1.226			1.696
	Betula platyphylla	6.333	14.508	22.987	24.394	9.056
	Populus davidiana	0.163	10.319	0.216		
Shrub layer	*Pinus pumila*			1.258	10.356	29.996
	Juniperus sibirica		2.511			3.968
	Alnus mandshurica			1.831	0.957	1.568
	Betula middendorfii					12.419
	Rhododendron dauricum	41.033	51.342	75.045	31.755	10.644
	Ledum palustre	42.111	38.159	11.675	36.660	11.361
	Vaccinium vitis-idaea	60.675	49.175	54.191	64.273	58.918
Herb layer	*Deyeuxia angustifolia*		20.317	16.662	20.666	
	Carex caespitosa		8.845	2.013	2.285	4.402
	Maianthemum bifolium	4.469	1.067	4.850	4.761	
	Pyrola incarnata	13.745		0.149		
	Saussurea amara	8.732	0.971	2.440	0.372	
	Saxifraga bronchialis					9.276
	Dryopteris fragrans					8.970
	Vicia pseudorobus	5.372	0.299	1.196		
	Iris ruthenica		1.000	3.640	0.570	

Note: a blank indicates that the species does not exist on this plot

3.2 Niche characteristics at the intermediate scale

At the intermediate scale, the niche breadths of *L. gmelinii* and *B. platyphylla* were widest in the tree layer (Table 4). In the shrub layer, the niche breadth of *V. vitis-idaea* was widest, followed by *R. dauricum* and *L. palustre*. In the herb layer, the niche breadth of *D. angustifolia* was widest. In general, the species with a wide niche breadth tend to have a high niche overlap with

Table 4 The Levins niche breadth (B_1) and Hurlbert niche breadth (B_2) of dominant species in *Rhododendron dauricum* plant communities at the intermediate scale

Layer	Species	B_1	B_2	Species	B_1	B_2
Tree layer	*Larix gmelinii*	2.145	0.708	*Populus davidiana*	1.431	0.132
	Pinus sylvestris	1.038	0.043	*Ledum palustre*	2.607	0.528
Shrub layer	*Pinus pumila*	2.125	0.159	*Vaccinium vitis-idaea*	2.805	0.844
	Alnus mandshurica	1.454	0.036	*Juniperus sibirica*	1.515	0.032
	Betula middendorfii	1.820	0.070	*Maianthemum bifolium*	1.668	0.190
	Rhododendron dauricum	2.740	0.662	*Vicia pseudorobus*	1.594	0.174
Herb layer	*Deyeuxia angustifolia*	1.904	0.363	*Carex caespitosa*	1.297	0.089
	Saussurea amara	1.564	0.134	*Iris ruthenica*	1.166	0.055
	Pyrola incarnata	1.493	0.142	*Saxifraga bronchialis*	1.021	0.046
	Betula platyphylla	2.147	0.706	*Dryopteris fragrans*	1.052	0.047

other species. There were higher niche overlaps between *L. gmelinii, B. platyphylla, R. dauricum, L. palustre,* and *V. vitis-idaea* (Table 5). For interspecific associations, the overall associations between communities were both positively correlated at 10 m × 10 m and 5 m × 5 m scales (*VR* > 1). Between *L. gmelinii, B. platyphylla, R. dauricum, L. palustre,* and *V. vitis-idaea*, there was also a positive correlation trend (expect for *L. gmelinii* and *B. platyphylla* at a 5 m × 5 m scale) (Table 6). Thus, the interspecific association of the integrated niche overlap demonstrates a tendency for mutual facilitation among the interspecific relationships of dominant species.

At the intermediate scale, elevation was the most dominant environmental factor, followed by soil nutri-ents. As a synthesis factor, elevation was significantly correlated with soil temperature, moisture, pH, TC, TP, and TK. In the tree layer, *L. gmelinii* and *B. platyphylla* appeared to be differentiated and complementary in terms of their resource utilization (Fig. 2). Specifically, the habitat of *L. gmelinii* tended to have an elevation gradient of 600–800 m and 1050–1200 m, a relatively shady slope, and a relatively higher soil nutrient (TC, TN, and TP). *B. platyphylla* was the opposite. Further, *P. davidiana* and *B. platyphylla* had relatively similar habitat conditions for soil pH, TC, TN, TP, and TK. In the shrub layer, the habitat of *P. pumila* tended to have a higher elevation gradient (900–1200 m) and more soil nutrients (TC, TN, and TP) (Fig. 3). *R. dauricum* and *L. palustre* were the opposite.

Table 5 The niche overlap index (O_{ik}) and curve average model (C_{ih}) of dominant species in *Rhododendron dauricum* plant communities at the intermediate scale

O_{ik} \ C_{ih}	1	2	3	4	5	6	7	8	9	10	11
1		0.053	0.517	0.083	0.366	0.140	0.122	0.218	0.572	0.563	0.736
2	0.125		0.057	0.193	0.077	0.087	0.089	0.077	0.079	0.101	0.068
3	0.494	0.109		0.145	0.300	0.085	0.151	0.109	0.683	0.577	0.702
4	0.136	0.120	0.234		0	0.273	0	0	0.223	0.203	0.142
5	0.534	0.228	0.354	0		0.127	0.076	0.381	0.072	0.148	0.208
6	0.266	0.088	0.155	0.325	0.096		0.012	0.186	0.031	0.021	0.060
7	0.215	0.220	0.334	0	0.118	0.012		0.091	0.025	0.031	0.040
8	0.385	0.181	0.244	0	0.290	0.123	0.090		0.031	0.064	0.118
9	0.628	0.124	0.762	0.413	0.098	0.088	0.110	0.096		0.440	0.665
10	0.643	0.186	0.659	0.324	0.173	0.032	0.492	0.078	0.461		0.525
11	0.841	0.205	0.794	0.310	0.336	0.144	0.169	0.217	0.689	0.590	

Notes: The number 1–11 represent *Larix gmelinii, Pinus sylvestris, Betula platyphylla, Populus davidiana, Pinus pumila, Juniperus sibirica, Alnus mandshurica, Betula middendorfii, Rhododendron dauricum, Ledum palustre,* and *Vaccinium vitis-idaea,* respectively

Table 6 The association coefficient (*AC*) of dominant species in *Rhododendron dauricum* plant communities at the intermediate scale

10×10 \ 5×5	1	2	3	4	5	6	7	8	9	10	11
1		0.008	−0.129[*]	0.007	−0.143[*]	0.012	−0.425[**]	−0.083	0.314[**]	0.128[**]	0.084
2	0.005		0.004	0.044[**]	−0.034	−1.000	0.026	0.099	0.343	0.326	0.020
3	0.003	−0.017		0.061[**]	−0.175[**]	0	−0.100	−0.352[**]	0.589[**]	0.042	0.388[**]
4	0.014	0.169[**]	0.029[*]		−1.000[**]	0.074[**]	−1.000[*]	−1.000[**]	1.000[**]	0.221	0.218
5	−0.039	−0.221	−0.108	−1.000[**]		0.088[**]	0.055[**]	0.315[**]	−0.499[**]	−0.011	0.113
6	0.023	0.093	0.001	0.192[**]	0.073		0.009	0.383[**]	−0.126[*]	−0.409[**]	0.001
7	−0.147	0.011	0.008	−1.000[*]	0.091[*]	0.039		0.286[**]	−0.110	−0.117	0.510
8	0.013	0.149	−0.171	−1.000[*]	0.314[**]	0.404[**]	0.255[**]		−0.321[**]	−0.060	−0.034
9	0.236	1.000	0.236	1.000	−0.474	−0.039	−0.039	−0.404		0.059[**]	0.364[**]
10	0.101[*]	0.496	0.011	0.529	−0.009	−0.128	−0.070	−0.038	0.026		0.831[**]
11	0.236	−0.096	0.236	−0.200	0.546	−0.039	1.000	0.007	0.483[**]	1.000[**]	

Notes: The number 1–11 represent *Larix gmelinii, Pinus sylvestris, Betula platyphylla, Populus davidiana, Pinus pumila, Juniperus sibirica, Alnus mandshurica, Betula middendorfii, Rhododendron dauricum, Ledum palustre,* and *Vaccinium vitis-idaea,* respectively. 10 × 10: 10 m × 10 m scale; 5 × 5: 5 m × 5 m scale; [*]: *P* < 0.05; [**]: *P* < 0.01
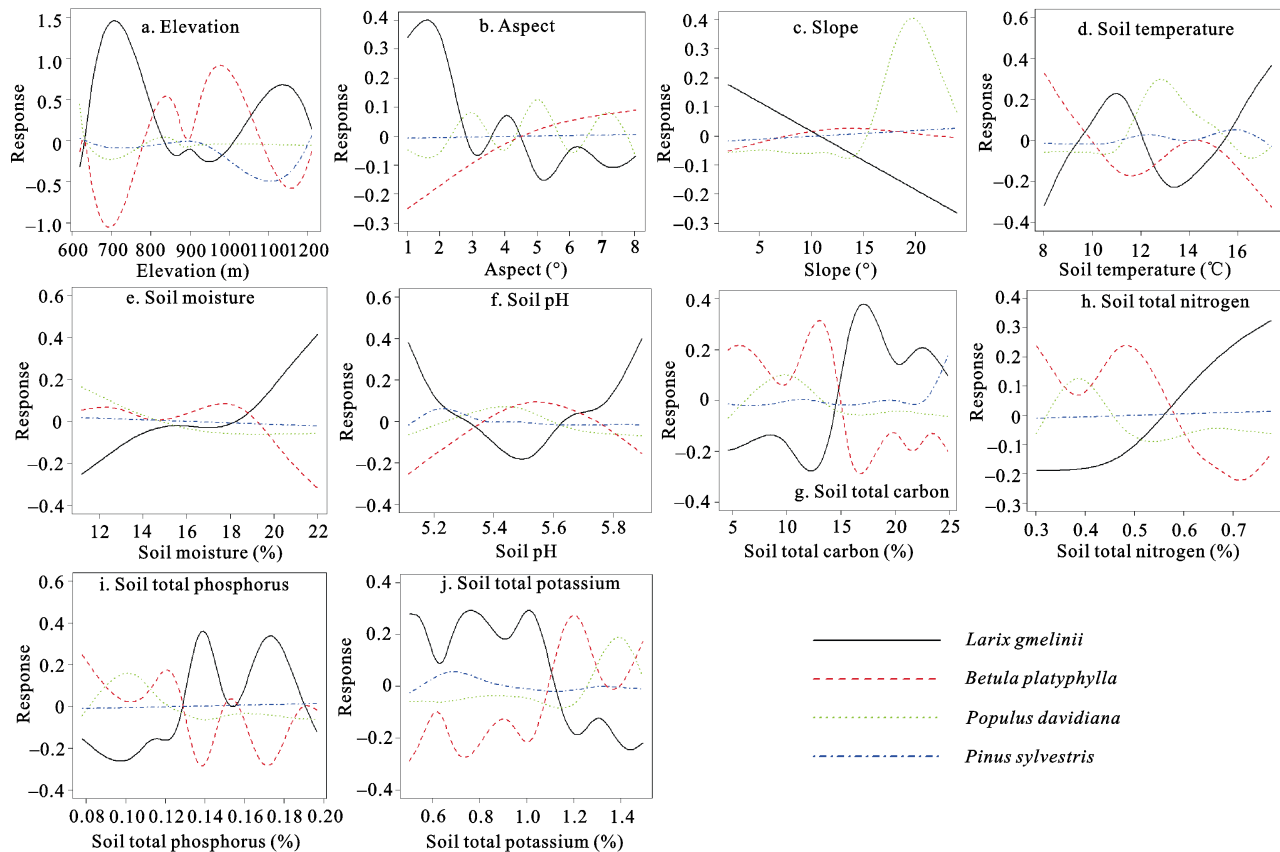
Fig. 2 Response of niche characteristics to the environmental factors of the dominant species of the tree layer at the intermediate scale. The *x*-coordinate is the value of the corresponding environmental factor. For aspect (b), the numbers '1–8' represent north (0°–22.5°, 337.5°–360°), northeast (22.5°–67.5°), northwest (292.5°–337.5°), east (67.5°–112.5°), west (247.5°–292.5°), southeast (112.5°–157.5°), southwest (202.5°–247.5°), and south (157.5°–202.5°); The *y*-coordinate is the eigenvalue calculated by the generalized additive model (GAM). The relevant variable are environmental factors, and the explanatory variable is the Importance Value (*IV*) of the species in the quadrats, *n* =180. The larger the eigenvalue of the *y*-coordinate, the greater the dominance of the species

The relationship between the local and intermediate scales was shown in two ways. One aspect was the relationship between *IV* and niche breadth. In this study, the species with a wide niche breadth tended to have a high *IV*. Conversely, the species with a high *IV* in one community did not necessarily have a wide niche breadth. This shows cases the lability of niche characteristics at the local scale. Another aspect was the relationship between environmental factors. At the local scale, environmental conditions tended to have similar elevations, aspects, and soil properties within a community. *L. gmelinii*, *B. platyphylla*, *R. dauricum*, *L. palustre*, and *V. vitis-idaea* were the absolute dominant species at the intermediate scale. Specifically, they had the widest niche breadth and a high niche overlap. Further, they were almost all positively correlated. In addition, there was a trend of differentiation along the environmental factor gradient for some species. Thus, for

niche characteristics, there was some degree of relationship between the local and intermediate scales, and the niche characteristics at the intermediate scale were relatively regular.

3.3 Niche characteristics at the regional scale

At the regional scale, *L. gmelinii*, *B. platyphylla*, *P. davidiana*, *P. sylvestris*, and *R. dauricum* were widely distributed in forest communities of the Da Hinggan Mountains, Xiao Hinggan Mountains, and Changbai Mountains (Fig. 4). *J. sibirica*, *A. mandshurica*, *L. palustre*, and *V. vitis-idaea* were mainly distributed in the north of the Da Hinggan Mountains and the main peak of the Changbai Mountains. *P. pumila* and *B. middendorfii* were mainly distributed in the north of the Da Hinggan Mountains. For the environmental factors, temperature and precipitation were the dominant factors limiting the distribution of species. For *P. davidiana*, *B. platyphylla*,
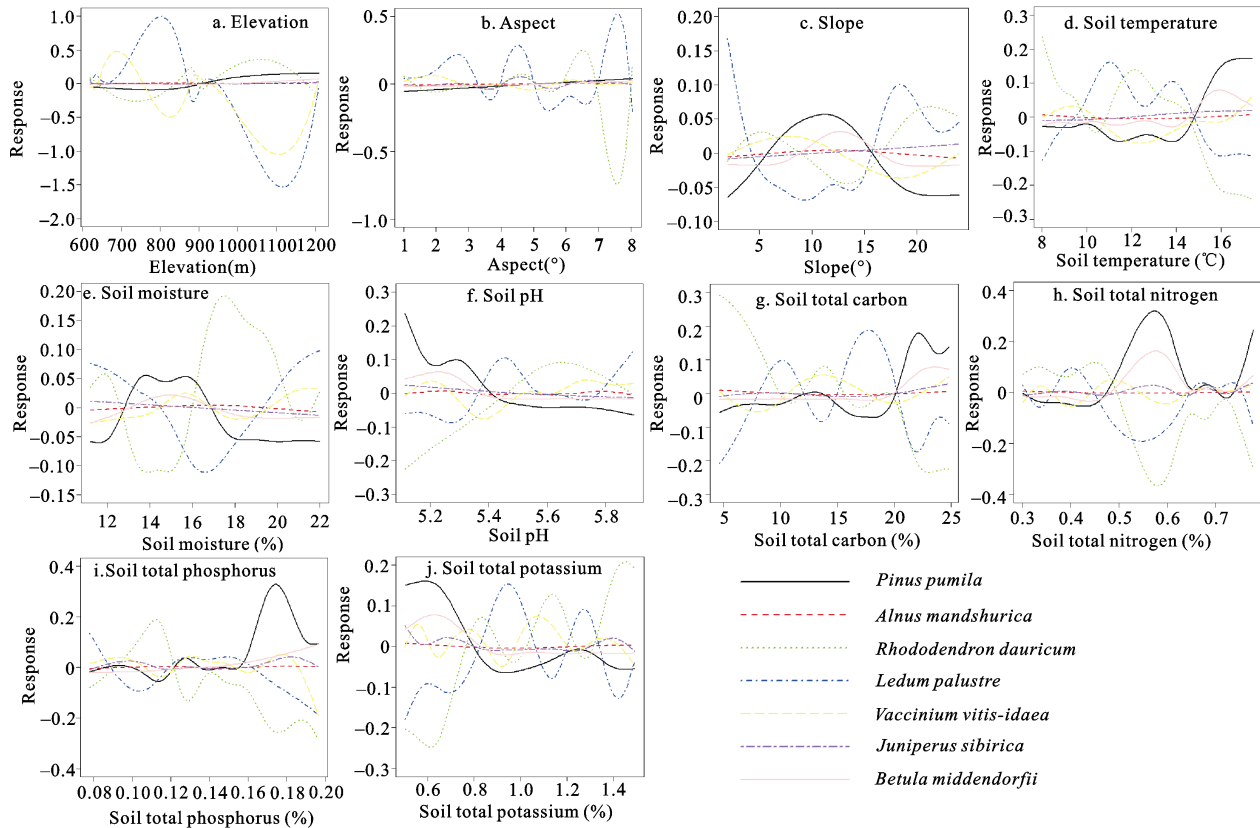
Fig. 3 Responses of niche characteristics to the environmental factors of the dominant species of the shrub layer at the intermediate scale. The *x*-coordinate is the value of the corresponding environmental factor. For aspect (b), the numbers '1–8' represent north (0°–22.5°, 337.5°–360°), northeast (22.5°–67.5°), northwest (292.5°–337.5°), east (67.5°–112.5°), west (247.5°–292.5°), southeast (112.5°–157.5°), southwest (202.5°–247.5°), and south (157.5°–202.5°); The *y*-coordinate is the eigen value calculated by the generalized additive model (GAM). The relevant variable are environmental factors, and the explanatory variable is the Importance Value (*IV*) of the species in the quadrats, *n* = 720. The larger the eigenvalue of the *y*-coordinate, the greater the dominance of the species

R. dauricum and *B. middendorfii*, the limiting environmental factor was low temperature (Bio 6, 9, 11). For *P. sylvestris* and *L. gmelinii*, the limiting environmental factor was mean temperature (Bio 1, 6, 8, 9, 10, 11). For *J. sibirica*, *A. mandshurica*, *V. vitis-idaea* and *L. palustre*, the limiting environmental factor was precipitation (Bio 12, 13, 14, 16. 17, 18, 19). For *P. pumila*, the limiting environmental factor was min precipitation (Bio 14, 17, 19).

The relationship between the intermediate and regional scales is shown as the relationship between niche breadth and geographic distribution. Generally, species with a wide niche breadth tend to have a wide range of distribution. Moreover, for widely distributed species, temperature is the limiting factor. Thus, for niche characteristics, there is some degree of relationship between the intermediate and regional scale, and niche characteristics at the intermediate scale also have some degree

of regularity.

4   Discussion

Multiple study scales allow for a more comprehensive analysis of ecological issues (Han et al., 2009; Wei et al., 2012). Based on our study results, the niche characteristics at the local, intermediate, and regional scales were both similar and different. A relationship existed between the local and intermediate scales, as well as between the intermediate and regional scales. The differences were in the features of the niche characteristics at the three scales. Specifically, the niche characteristics at the local scale were various and labile, and the niche characteristics at the intermediate and regional scales were relatively regular. There was some degree of consistency between these results and those of previous studies from an evolutionary perspective (Silvertown et al., 2006a; 2006b).
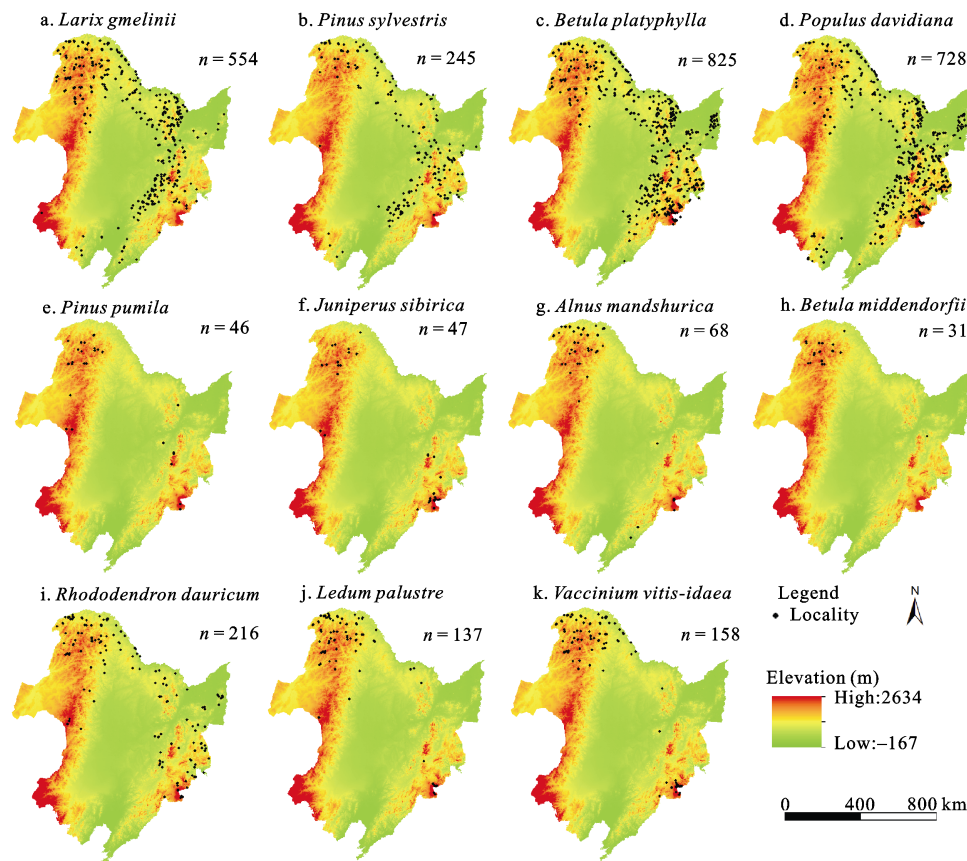
Fig. 4 Distribution of the dominant species of *Rhododendron dauricum* plant communities in Northeast China. '*n*' is the number of the locality of the species

4.1 Mechanism of lability for the niche characteristics at the local scale

Silvertown et al. (2006b) studied two mesotrophic grassland communities in England and found that species coexisting in the same habitat tend to have a similar *β* niche (at the intermediate scale) and a different *α* niche (at the local scale). Thus, the mechanism of lability for the niche characteristics at the local scale might be related to interspecific interactions and the microenvironment generated by vegetation. In the process of community assembly, the environment provides the filtration for plant species. Conversely, plant species can also affect the environment (through niche construction) (Kylafis and Loreau, 2008; Mori et al., 2013; Laliberté et al., 2014). At the local scale—more precisely, in a community—the canopy of vegetation can reduce light illumination and air temperature and increase air humidity. Furthermore, the litters and roots of vegetation can affect soil conditions (Gómez-Aparicio et al., 2004; Brooker et al., 2008). As a consequence, due to the ex-

istence of the microenvironment, the internal environment of a community is complex and labile, even under similar habitat conditions. In this study, the same elevation gradients could be considered to be similar habitats. Between plot A and B (600 m), *J. sibirica* only existed in the latter. Further, the dominant species of the herb layer of plot A was *P. incarnate*, and that of plot B was *D. angustifolia* because the canopy density of plot A was higher.

4.2 Niche and interspecific relationships at the intermediate scale

The relationship between the intermediate and regional scales is shown as the relationship between niche breadth and geographic distribution. Niche breadth reflects the adaptability and tolerance of species to a variable environment. In other words, the species with a wide niche breadth tend to have a wide range of distributions (Mason et al., 2011; Boulangeat et al., 2012; Slatyer et al., 2013; Hirst et al., 2017; Kambach et al.,

2019). In this study, *L. gmelinii*, *B. platyphylla*, *R. dauricum*, *L. palustre*, and *V. vitis-idaea* were the dominant species with widest breadths and had relatively wide distributions. Worldwide, *Pinaceae*, *Betulaceae*, and *Ericaceae* are all wide spread families. Many studies indicate that niche breadth is related to genetic components (the niche width-variation hypothesis). More specifically, species with a wide niche breadth tend to have high genetic variation or generic genotypes with high phenotypic flexibility and plasticity to adapt to various habitats (Babbel and Selander, 1974; Schmid, 1984; Herrera et al., 2012; Fajardo and Siefert, 2019).

At the intermediate scale, topography and soil are the main environmental factors that differentiate between habitat conditions (Silvertown et al., 2006b; Anthwal et al., 2008; Fajardo and Siefert, 2019). We analyzed the effects of ten topography and soil factors and found that their niche characteristics were regular. More precisely, we found relatively clear differentiation and similarities between the resource dimensions. These were actually the embodiment of the inherent biological and ecological traits of the plant species (Lawesson and Oksanen, 2002). Compared with *B. platyphylla*, a typical early successional species, *L. gmelinii* had more competitive morphological characteristics (height, canopy, DBH, *etc.*) and thus occupied the more favorable dimensions of soil resources. Similarly, *P. pumila* had more competitive morphological characteristics (height, canopy, etc.) in the shrub layer but required a certain amount of space and light; thus, it was more dominant in communities with sparse trees (with a relatively higher elevation). Therefore, the mechanism for the regularity of niche characteristics at the intermediate scale is related to the inherent biological and ecological traits of species and the environmental gradients of habitats.

With the ability to utilize multiple resources, broad niche breadth species tend to occupy the same resource dimensions as other species, which indicates a niche overlap. One suggestion is that the niche overlap of closely related species might be reduced (Wilson and Lee, 1994; Webb et al., 2002). Furthermore, due to their common phylogenetic origins, closely related species (one genus) tend to have similar ecological traits and utilize similar resources; thus, they will compete more fiercely. In this study, the dominant species of the same genus (*Pinus*: *P. sylvestris* and *P. pumila*; *Betula*: *B. platyphylla* and *B. middendorfii*) had a relatively low niche overlap ($O_{ik} < 0.25$, $C_{ih} < 0.11$). Conversely, partial species of the same family (*Pinaceae*: *L. gmelinii* and *P. pumila*; *Ericaceae*: *R. dauricum*, *L. palustre*, and *V. vitis-idaea*) tended to have a relatively high niche overlap. The high niche overlap between these species is related to their phylogenetic relationships or the inherent niche breadth of species, which requires further study.

A high niche overlap indicates a high similarity of the resources used by species. Nonetheless, is there intense competition or facilitation between these species? Interspecific association has provided a new way to comprehensively analyze interspecific relationships. At 10 m × 10 m and 5 m × 5 m scales, *R. dauricum* and *V. vitis-idaea*, *L. palustre* and *V. vitis-idaea* were all significantly positively correlated. At a 5 m × 5 m scale, *L. gmelinii* and *B. platyphylla* were significantly negatively correlated (albeit not strongly). *L. gmelinii* and *R. dauricum*, *B. platyphylla* and *R. dauricum*, and *B. platyphylla* and *V. vitis-idaea* were all significantly positively correlated. Therefore, except for *L. gmelinii* and *B. platyphylla*, the dominant species showed a tendency to engage inmutual facilitation, which shows that the community of *R. dauricum* was relatively stable. Moreover, the overall association between the species in each community was positive correlated ($VR > 1$), which again proves the stability of each community (Hurlbert, 1969; Callaway et al., 2002). Previous studies indicated that harsh habitat conditions may be one of the reasons for the facilitation and reciprocity between species (conditions such as low temperature, drought, and infertility) (Padilla and Pugnaire, 2006; Brooker et al., 2008; Wright et al., 2015). Accordingly, in Northeast China, a low temperature has always been one of the main factors limiting plant survival and growth, especially in mountainous areas.

4.3 Impact of climate factors on species distribution at the regional scale

At the regional scale, climate is the dominant factor limiting the distribution of plant species (Morin and Lechowicz, 2013; Gouveia et al., 2014; Kotta et al., 2014). In this study, temperature was the main climatic factor effecting the distribution of the four dominant species in the tree layer. Strong cold resistance might be one of the reasons for their widespread distribution in Northeast China (the minimum temperatures of the coldest month were −25 to −29 ℃, and the mean tem-

peratures of the coldest quarter were −17 to −21 ℃). Moreover, the limiting factor for the distribution of both *B. platyphylla* and *P. davidiana* was low temperature, as the values of their temperatures were very close. At the intermediate scale, *P. davidiana* and *B. platyphylla* had relatively similar habitat conditions related to soil pH, TC, TN, TP, and TK. Thus, there was some degree of consistency in the results between the intermediate scale and the regional scale. Low temperature was also a limiting factor for the distribution of *R. dauricum* and *B. middendorfii*, and the cold resistance of latter was stronger than that of the former (the lowest temperatures of the coldest month were −31 and −37 ℃; the mean temperatures of the coldest quarter were −22 and −27 ℃). This may be one of the reasons why temperature was dominant in communities at a relatively higher elevation (plot E). For the other five dominant species in the shrub layer, precipitation was the main limiting factor. The annual precipitation of *L. palustre* and *V. vitis-idaea* was relatively less. Thus, these two species have strong drought resistance and lower requirements for water, which may be one of the reasons for their relatively broad niche breadth and wide distribution.

5   Conclusions

In this study, we analyzed the niche characteristics of the *R. dauricum* plant communities in Northeast China at local, intermediate, and regional scales. The niche characteristics at the three scales were both related and different. The niche characteristics at the local scale were various and labile, and the niche characteristics at the intermediate and regional scales were relatively regular. This shows some degree of consistency with previous studies that used an evolutionary perspective. The mechanism of action is related to the differences in dominant environmental factors. In addition, the integration of niche overlap and interspecific association demonstrate interspecific relationships more accurately. For relatively stable communities, there are relationships of mutual facilitation between dominant species, including trees and shrubs. Moreover, *R. dauricum* plays an important role for maintaining temperate forest community stability in Northeast China. Therefore, we suggest that shrubs should also be considered in temperate forest management. Our study verifies the concepts of niches at multiple spatial scales in temperate forest

communities and could be used as a reference for future niche studies.

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