Research paper

Ecological and habitat ranges of orchids in the northernmost regions of their distribution areas: A case study from Ural Mountains, Russia

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ABSTRACT

The Orchidaceae, which is one of the most interesting families of angiosperms, contains a large number of rare species. Despite their acknowledged importance, little attention has been paid to the study of orchids distributed in northern territories. In this study, we determined the syntaxonomical diversity and ecological parameters of orchid habitats in two of Europe's largest protected areas, the Pechoro-Ilychsky Reserve and the Yugyd Va National Park (northeastern European Russia), and then compared our findings to those in other parts of orchid distribution ranges. For this purpose, we studied 345 descriptions of plant communities (releves) containing species from Orchidaceae and defined habitat parameters using Ellenberg indicator values with the community weight mean approach, nonmetric multidimensional scaling (NMS), and relative niche width. We found that orchids were distributed in eight habitat types and 97 plant associations. The largest number of orchid species is found in forest communities. Half of the orchid species under study occur in the mires and rock habitats with open vegetation. Several orchids consistently occur in areas disturbed by human activity. In addition, our study indicates that the main drivers of orchid distribution across the vegetation types are light and soil nitrogen. Our analysis of the ecological parameters of orchid habitats indicates that some orchid species can be classified as habitat specialists that are confined to a relatively narrow ecological niche in the Urals (e.g., *Goodyera repens, Cypripedium guttatum* and *Dactylorhiza maculata*). Several other species (e.g. *Neottia cordata* and *Dactylorhiza fuchsia*) grow under diverse ecological parameters.

1. Introduction

The Orchidaceae, which contains 28,000 species (Fay, 2018), is one of the largest families of flowering plants. Orchids exhibit various peculiarities (e.g., mycosymbiotrophism, high specialization of pollination) that narrow their ecological range and reduce competitiveness. Accordingly, orchids are sensitive to changes in the environment and are usually the first to drop out of plant communities in response to anthropogenic disturbances (Swarts and Dixon, 2009; Fay et al., 2015), making these species excellent bioindicators of ecological quality (Gale et al., 2018). Recently, the total number of orchids has decreased worldwide (Kull and Hutchings, 2006; Ghorbani et al., 2014; Liu et al., 2015; Vogt-Schilb et al., 2015; Wraith

and Pickering, 2018, 2019; Štípková and Kindlmann, 2021). Successful conservation management of orchids requires knowledge of the ecological preferences and distribution patterns of plant species (Margules and Pressey, 2000; Djordjević et al., 2016a).

Orchids grow in a wide variety of habitats (Vakhrameeva et al., 2008; Djordjević and Tsiftsis, 2020). Recent studies on the ecological and phytocoenotical preferences of individual species show that the orchid habitats may vary across their distribution ranges (Kull, 1999; Jersáková et al., 2011; 2015; Meekers et al., 2012; Kotilínek et al., 2015, 2018). According to the "abundant-centre hypothesis", species in the center of the range most often inhabit a great variety of vegetation types, whereas on the edges they mainly grow in a limited number of plant communities (Sagarin and Gaines, 2002). Although many researchers have emphasized the importance of studying vegetation to determine patterns of the orchid distribution and abundance (Tsiftsis et al., 2008; Djordjević et al., 2016a, b, 2020a), orchid habitat diversity across entire distribution ranges has been scarcely studied. A comprehensive exploration of orchid

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phytocoenology will give us better understanding of orchid conservation priorities. It will also allow us to identify habitats that require environmental protection and to manage the conservation activities for this vulnerable group of plants more effectively.

Protected areas are crucial for preserving natural populations of rare species, including orchids (Zhou et al., 2021). Protected area size is extremely important (Schödelbauerová et al., 2009). Two of the largest protected areas in Europe, the Pechoro-Ilychsky Reserve and Yugyd Va National Park, are located in the Russian European Northeast on the western slopes of the Northern and Subpolar Urals. These protected areas are practically unaffected by human activities and contain the largest virgin forests (32,800 km^2) in Europe, which have been designated on the UNESCO World Natural Heritage List as the "Virgin Forests of Komi".

The northern part of the Ural Mountains is remote from roads and settlements. As a result, it is difficult to carry out long-term observations of ecological parameters, and single measurements do not reliably reflect long-term habitat conditions. Indicator values based on the ecological preferences of plant species provide more general environmental data important for plant population analysis (Ellenberg et al., 1992; Diekmann, 2003; Ozinga et al., 2013; Sizonenko et al., 2020; Cîșlariu et al., 2021). To successfully manage rare species populations, it is crucial to study not only plant species composition, but also other vegetation and ecological parameters, such as dominant species complexes, tree productivity, understorey structure, soil wetness and fertility. Dominant classification is a habitat site type classification approach that groups habitat sites based on different parameters of all vegetation layers and abiotic factors (Skovsgaard and Vanclay, 2008; Pohjanmies et al., 2021). This approach is used mainly for forest ecosystem studies, as forests are dynamic and vary in multiple ways and at various scales (Fomin et al., 2017). However, for all types of boreal vegetation, plant associations revealed by dominant classification correspond to specific plant communities worked on by conservationists and population biologists.

According to the literature, there are 20 species of orchids in the Northern and Subpolar Urals, and almost all of them grow on the northern limits of their natural ranges. Studies of orchid species have been carried out in this region since 2000 (Kirillova, 2010, 2015). However, little attention has been paid to the phytocoenotical and ecological confinement of these species (Plotnikova et al., 2010; Kirillova et al., 2018). Here, we hypothesized that for most orchids in the study area the number of habitats occupied and the ecological amplitudes of habitats are narrower in northern populations than in the main parts of their ranges. To test this hypothesis, we analyzed the syntaxonomical diversity and ecological parameters of orchid habitats in northern regions of the Ural Mountains and compared these findings to those of orchid habitats in other regions of their distribution ranges.

2. Materials and methods

2.1. Study area

The study area is located in the northeastern European Russia within Komi Republic (Fig. 1). It includes two of the largest European protected areas – Pechoro-Ilychsky Reserve and Yugyd Va National Park. The study area is mostly situated in the Northern and Subpolar Urals. It occupies 400 km from north to south with a total area of over 2.6 million hectares. The climate is severe and sharply continental with a prevalence of unstable and humid weather. Mean annual temperature ranges from −1 °C (Northern Urals) to −6 °C (Subpolar Urals). The coldest month is January with a mean temperature ranging between −16 °C and −21 °C; the warmest month is July

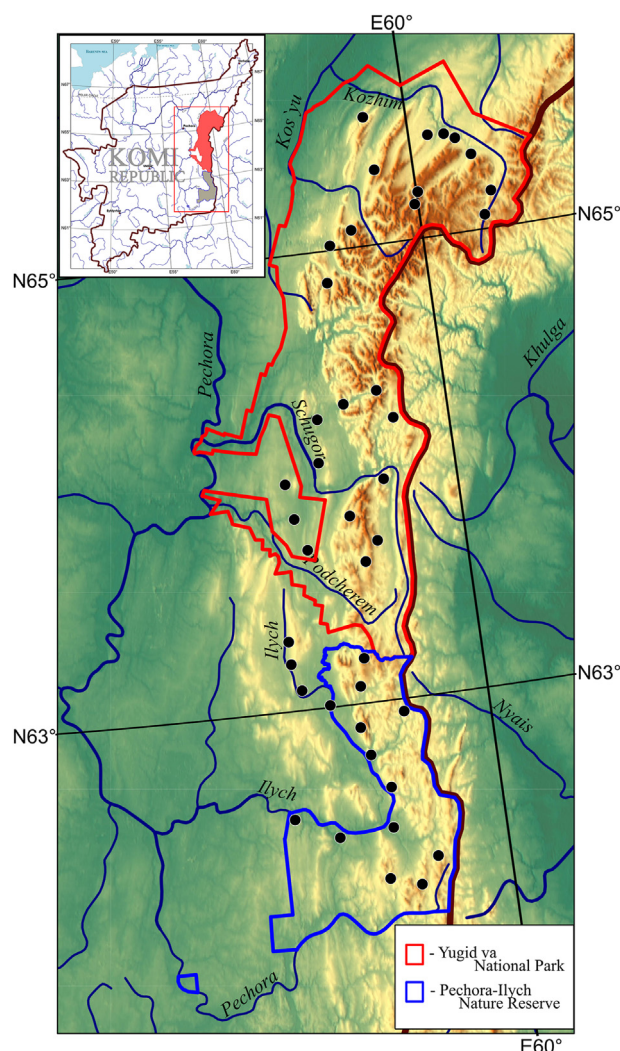**Fig. 1.** Location of the study area (black dots – study sites).

(13–16 °C). Annual precipitation varies from 900 mm in the Northern Urals to 1100 mm in the Subpolar Urals (Kornienko, 2011).

The main vegetation types are plain and mountain forests and mountain tundra. Mires are less common, but also cover large areas (Taskaev, 2006). Plant communities of meadows and shrubs (mainly willows) occur in the floodplains and river valleys. More than half of the study area is covered by forest, mostly by *Picea obovata* Ledeb. *Abies sibirica* Ledeb. and *Betula pubescens* Ehrh. are often prevalent in the mountain forests in the Northern Urals. Northward, *Larix sibirica* Ledeb. is dominant in tree stands in large areas of the mountain landscapes.

2.2. Data collection

The full data set on vegetation of the study area contains 3500 descriptions of plant communities (releves) made between 1987 and 2021. At each study site (Fig. 1), the plots were positioned randomly and along the main ecological gradients to represent all plant associations. The releves were made and classified using standard methods of the dominant vegetation classification approach (Neshataev, 2001; Ipatov and Mirin, 2008; Fomin et al., 2017). We described the composition of the tree layer. Undergrowth and herb-dwarf shrub layers were characterized by the relative abundance of species. In this research, we have studied 345

Table 1
Diversity of orchid habitats in the Northern and Subpolar Urals compared to entire species ranges.

Species	Number of releves	Number of plant associations	Habitat types, Northern and Subpolar Urals	Habitat types, entire species range[a]
Coeloglossum viride (L.) Hartm.	33	22	Riverside, Meadow, Forest, Bush, Tundra, Rock	Mire, Riverside, Meadow, Forest, Bush, Tundra, Grassland, Heath
Corallorhiza trifida Châtel.	9	7	Mire, Forest	Mire, Meadow, Forest, Bush, Tundra
Cypripedium calceolus L.	13	5	Forest, Rock, Technogenic Habitats	Mire, Meadow, Forest, Bush, Rock, Grassland
Cypripedium guttatum Sw.	8	5	Forest	Forest, Bush, Grassland, Rock
Dactylorhiza fuchsii (Druce) Soó	69	35	Mire, Meadow, Riverside, Forest, Anthropogenically Disturbed Habitats	Mire, Meadow, Forest, Grassland, Tundra
Dactylorhiza maculata (L.) Soó	31	13	Mire, Forest	Mire, Meadow, Forest, Bush, Grassland, Tundra, Heath
Dactylorhiza traunsteineri (Saut. ex Rchb.) Soó	12	8	Mire, Meadow, Forest	Mire, Meadow, Bush, Tundra, Riverside
Epipactis atrorubens (Hoffm.) Besser	13	5	Forest, Rock	Meadow, Bush, Forest, Rock
Goodyera repens (L.) R. Br.	72	25	Forest, Rock	Forest, Bush, Heath
Gymnadenia conopsea (L.) R. Br.	15	9	Mire, Forest, Rock, Anthropogenically Disturbed Habitats	Mire, Meadow, Bush, Forest, Grassland, Tundra, Rock
Neottia cordata (L.) Rich.	146	48	Mire, Riverside, Forest, Bush	Mire, Meadow, Bush, Forest, Tundra, Heath, Dunes
Neottia ovata (L.) Bluff and Fingerh.	11	8	Mire, Forest	Mire, Meadow, Bush. Riverside, Forest, Grassland, Dunes, Anthropogenically Disturbed Habitats
Platanthera bifolia (L.) Rich.	4	3	Forest	Meadow, Bush, Forest
Pseudorchis albida (L.) Á. Löve et D. Löve	1	1	Forest	Mire, Meadow, Bush, Forest, Grassland, Tudra, Anthropogenically Disturbed Habitats

[a] According to Kull (1999); Jersáková et al. (2011); Meekers et al. (2012); Vakhrameeva et al. (2008); Kotilínek et al. (2015, 2018); Kühn et al. (2019); Kirillova and Kirillov (2021); etc.

releves, containing species from the Orchidaceae family (Appendix 1). The most releves with Orchids were obtained in forests (241 releves). Orchids were present in releves in mires (28), meadows (26), sloping riversides (14), rock habitats (10), anthropogenically disturbed habitats (8), bushes (6), and mountain tundra (3). The size of releve in the forest was 400 m^2, in mountain tundra, 25 m^2, and 100 m^2 in other habitat types.

To compare our data with those from other parts of the orchid species distribution ranges, we used information from published studies (Kull, 1999; Jersáková et al., 2011, 2015; Meekers et al., 2012; Vakhrameeva et al., 2014; Kotilínek et al., 2015, 2018; Djordjević and Tsiftsis, 2020 and many others).

2.3. Data analysis

Ecological parameters of habitats (soil moisture, soil nitrogen content, soil acidity, and illumination) were defined by Ellenberg indicator values (Ellenberg et al., 1992). For each releve, the ecological parameters were calculated by the community weight mean approach (Lavorel et al., 2008). The orchid releves have been ordinated by nonmetric multidimensional scaling (NMS) based on the Bray distance. The modified permutation model envfit.iv (Zelený and Schaffers, 2012) was used to fit the Ellenberg values to ordination diagrams. The beta diversity of orchid species was estimated by the number of plant associations where these species occur and by the niche width index (θ value) (Fridley et al., 2007). Cluster analysis was performed using the Bray similarity index and the group mean approach (UPGMA). All calculations were made in the R 4.0.5 with 'vegan' (Oksanen et al., 2018), and 'MASS' (Venables and Ripley, 2002) packages.

3. Results

3.1. Syntaxonomical characteristics and relative niche widths of orchids

In total, 14 orchid species were found in the analyzed set of releves (Table 1). The most common species were *Neottia cordata* (43% of releves), *Goodyera repens* (20%) and *Dactylorhiza fuchsii* (20%). *Pseudorchis albida* was present at a single plot. The orchids were found in eight habitat types and 97 plant associations (Appendix 2). The largest number of orchid species was contained in the following associations: *Menyanthoso-sphagnosum*, *Piceetum myrtilloso-hylocomiosum*, *Piceetum ruboso saxatilis-hylocomiosum*, *Piceetum equisetoso-sphagnosum*, and *Betuletum menyanthoso-sphagnosum* (6 species in each).

Coeloglossum viride, *Dactylorhiza fuchsii* and *Gymnadenia conopsea* can be considered as a group of species with a wide phytocoenotical range (Table 1; Fig. 2) and relative niche width (Fig. 3). At the same time, these species differed by their distribution patterns across the habitat types and plant associations (Figs. 2 and 3; Appendix 2). *D. fuchsii* occurred in a large number of releves and associations, mostly in the forest and meadow plant communities with well-developed herb layers, including associations of *Filipendulosum ulmariae*, *Calamagrostiosum purpureae*, and *Betuletum calamagrostiosum purpureae*. The species was found in anthropogenically transformed habitats and in mires.

Coeloglossum viride occurred at lower frequencies and preferred forest communities with the well-developed green moss cover (e.g., *Piceetum ruboso saxalilis-hylocomiosum*). In the mountains, *C. viride* was found in mountain meadow communities (*Geranioso-Calamagrostiosum purpureae*) and mountain tundra (*Myrtilloso-hylocomiosum*, *Avenelloso-hylocomiosum*, and *Vaccinioso-cladinosum*). Only two of 33 releves were established in plant communities with sphagnous moss cover.

Gymnadenia conopsea was found less frequently than was either *Dactylorhiza fuchsii* or *Coeloglossum viride*. *G. conopsea* inhabits two contrasting habitat types and plant associations (Fig. 2). The first group is the watershed mires (*Eriophoroso-carycoso-sphagnosum*, *Menyanthoso-sphagnosum*) and water-logged forests (*P. equisetoso-sphagnosum*, *Pinetum menyanthoso-sphagnosum*). The second group includes slope and rock limestone habitats (*P. ruboso saxalilis-hylocomiosum*, *Montano-Laricetum betuloso nanae-vaccinioso-hylocomiosum* and rock plant assemblages).

Two species, *Neottia cordata* and *Goodyera repens*, are widely represented in the vegetation of the study area (Table 1; Fig. 2;
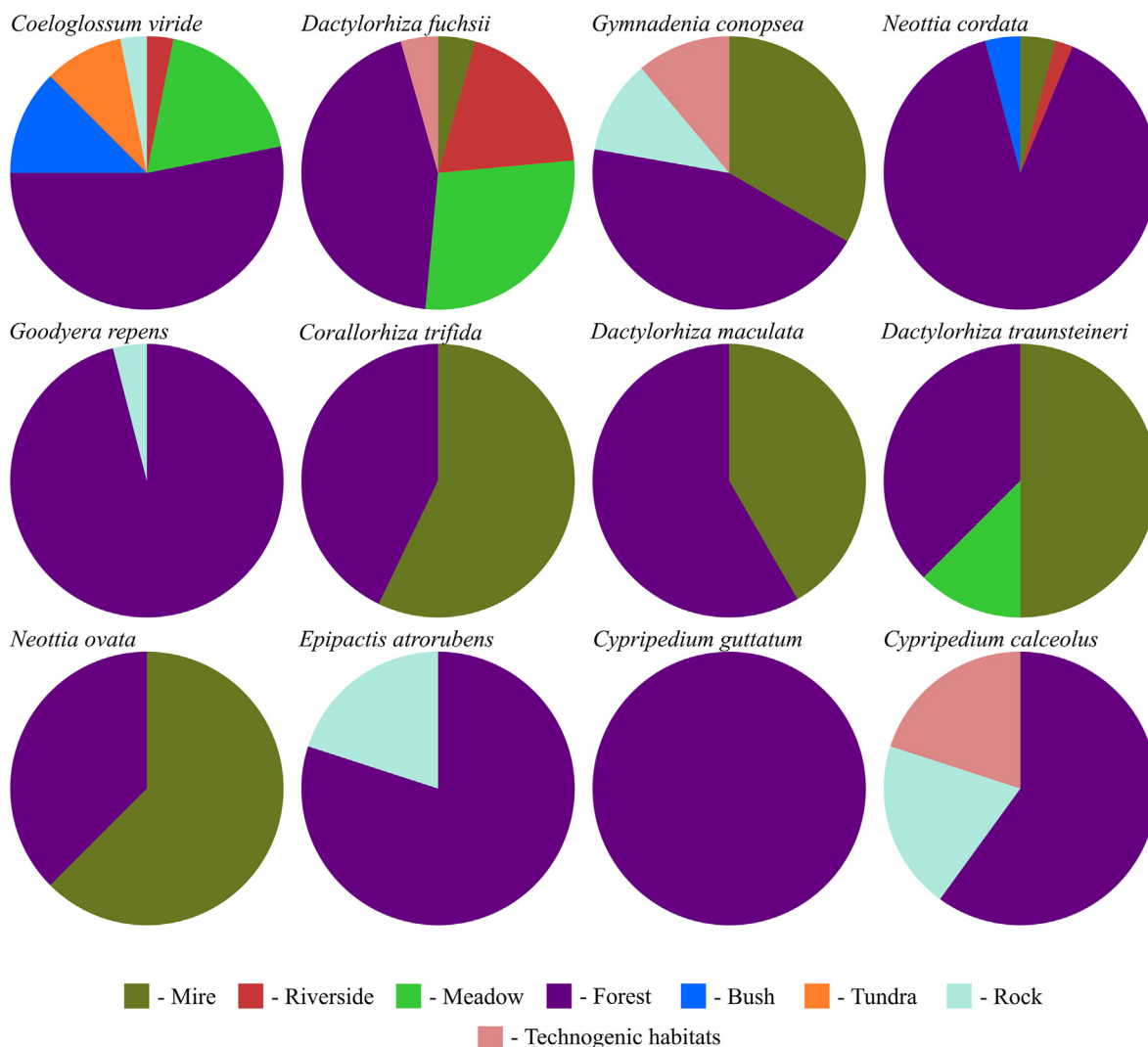
Fig. 2. Distribution of plant associations with orchids across habitat types.

Appendix 2), but their habitat range is limited (Fig. 3). In fact, they are the forest orchid species. *N. cordata* was noted in four habitat types, but 140 from 146 releves were made in the forest communities, mostly of plant associations of *P. myrtilloso-hylocomiosum*, *P. equisetoso sylvatici-sphagnosum*, *P. mytrilloso-sphagnosum*, *Abietetum phegopteridoso-dryopteridosum expansae,* and *A. myrtilloso-hylocomiosum*. *G. repens* was noticed in two habitat types, however,

Fig. 3. The relative niche widths (θ values) for orchid species. Black points − means of θ values. Lines − 95% confident intervals.

the releves were also located mostly in the forest with a predominance of green moss cover (*P. myrtilloso-hylocomiosum*, *P. gymnocarpioso-hylocomiosum*, *Betuletum vaccinioso-hylocomiosum*, *Populetum tremulae-vaccinioso-hylocomiosum*).

Species that preferred water-logged habitats included the "mire" orchids *Corallorrhiza trifida*, *Dactylorhiza maculata*, *Dactylorhiza traunsteineri* and *Neottia ovata* (Figs. 2 and 3; Appendix 2). Among these species, *D. maculata* occurred most frequently (Table 1) but had the lowest niche width (Fig. 3). The "mire" orchids were present mainly in oligotrophic mires (*Eriophoroso-carycoso-sphagnosum*, *Carycoso rostratae-sphagnosum*) and water-logged pine and spruce forests (*Pinetum eryophoroso-sphagnosum*, *P. carycoso-sphagnosum*, *P. equisetoso-sphagnosum*). *D. traunsteineri* was found in 12 releves with eight plant associations (Table 1; Appendix 2). It was common in the mire communities (*Carycoso-sphagnosum*, *Eriophoroso-carycoso-sphagnosum*, and *Menyanthoso-sphagnosum*) and water-logged forests (*Piceetum-equisetoso sylvatici-sphagnosum*, *B. menyanthoso-sphagnosum*). *C. trifida* and *N. ovata* occurred at similar frequencies (Table 1), with similar phytocoenotical preferences (Fig. 2) and niche widths (Fig. 3). These species occurred mainly in the releves of oligotrophic (*Carycoso rostratae-sphagnosum*, *Carycoso-sphagnosum*) and mesooligotrophic (*Menyanthoso-sphagnosum*) mires, and sphagnous spruce and birch forests (*P. equisetoso sylvatici-sphagnosum*, *B. menyanthoso-sphagnosum*).
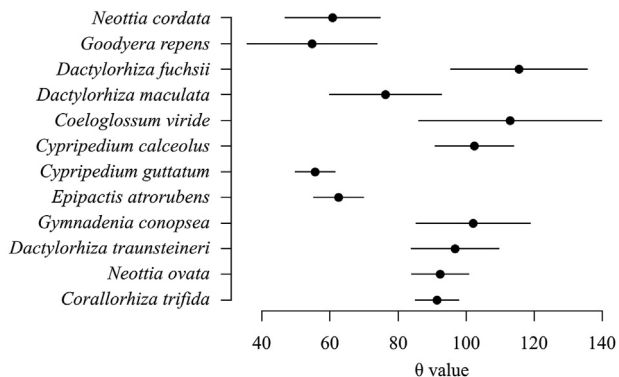
Three orchid species (*Epipactis atrorubens*, *Cypripedium calceolus* and *Cypripedium guttatum*) had an average occurrence in the study area (Table 1) and they were common in the sloping forests and rock plant assemblages (Appendix 2). *E. atrorubens* was found in spruce (*P. ruboso saxatilis-hylocomiosum*), aspen (*P. tremulae ruboso saxatilis-hylocomiosum*, *P. tremulae rubosum saxatilis*) and larch (*Montano-L. betuloso nanae-vaccinioso-hylocomiosum*) forests. Seven of 13 releves were located in scarce plant communities of rock habitats (Appendix 2). *C. guttatum* was common in the closed forest stands on river slopes. This species was present at high frequencies in spruce (*P. ruboso saxatilis-hylocomiosum*) and birch (*Betuletum ruboso saxatilis-hylocomiosum*) forests. The habitat range of *C. calceolus* was wider than that of *E. atrorubens* and *C. guttatum* (Figs. 2 and 3). *C. calceolus* occurred in three habitat types (Table 1) and preferred scarce rock plant communities (Appendix 2). It sometimes emerged in slope spruce forests (*Piceetum oxalidosum*), larch forests (*Montano-L. betuloso nanae-vaccinioso-hylocomiosum*) and water-logged birch forests (*B. menyanthoso-sphagnosum*). In addition, *C. calceolus* grows in anthropogenically transformed areas.

3.2. Ecological parameters of orchid habitats

According to the Ellenberg values (Appendix 3), all orchid species under study grow in the wet habitats, ranging from green moss forests with normal soil humidity to water-logged mires. The studied species were not demanding to the soil nitrogen richness. Most of them grow on low-acid soils.

The NMS ordination of orchid habitats based on ecological factors showed illumination (L) to be the main factor, distinguishing releves with different orchid species (Fig. 4; Table 2). Habitats of *Dactylorhiza maculata* were located in areas of higher moisture and illumination, while *Neottia cordata*, *Goodyera repens* and *Cypripedium guttatum* releves formed a clear cluster in areas of more shaded environment. The releves with *Dactylorhiza fuchsii* differed from those with *D. maculata* along the N and R vectors.

4. Discussion

4.1. General patterns of orchid's distribution across the habitat types

In this study, orchid species were found in 10% of plant communities in the Pechoro-Ilychsky Reserve and Yugyd Va National Park in the Northern and Subpolar Urals (345 of 3500 releves). The study area contained fourteen orchid species (59% of all orchids in Komi Republic), which is a rather large number, considering that the study area represents the northern boundary of most orchid species ranges. This finding is important for management of the Pechoro-Ilychsky Reserve and Yugyd Va National Park. Most orchid species grow in forest communities, which are the prevalent vegetation type in the study region. Compared to open types of habitat, forest stands create more stable environments, indicating that temperate forests across Russia may provide optimal conditions for many orchid species (Vakhrameeva et al., 2008).

The forest plant association *Piceetum myrtilloso-hylocomiosum* contains the largest number of orchids. This finding is consistent with several studies of European orchids, which have revealed that many species inhabit spruce forests (Delforge, 2006; Vakhrameeva et al., 2008; Lõhmus and Kull, 2011; Tsiftsis and Antonopoulos, 2017; Djordjević et al., 2020b). Additionally, in our study, forest orchid species include those preferring water-logged forest communities (e.g., plant associations *P. equisetoso-sphagnosum*, *B. menyanthoso-sphagnosum* etc.) and afforested river slopes (*P. ruboso saxatilis-hylocomiosum*, *Montano-L. betuloso nanae-vaccinioso-hylocomiosum* etc.). Moreover, half of the orchid species
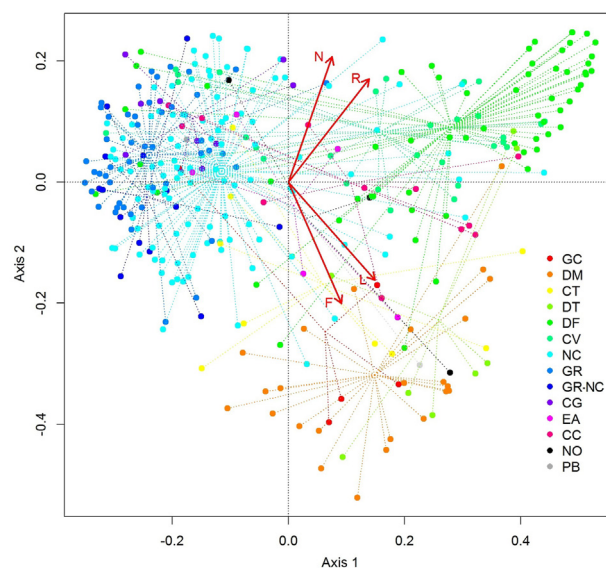

Fig. 4. Results of applied nonmetric multidimensional scaling (NMS) of orchid releves. Colored points, releves; red vectors, ecological parameters: L — illumination; R — soil acidity; N — soil nitrogen; F — moisture. GC — *Gymnadenia conopsea*, DM — *Dactylorhiza maculata*, CT — *Corallorhiza trifida*, DT — *Dactylorhiza traunsteineri*, DF — *Dactylorhiza fuchsii*, CV — *Coeloglossum viride*, NC — *Neottia cordata*, GR — *Goodyera repens*, GR-NC — *Goodyera repens* + *Neottia cordata* (co-occurrence), CG — *Cypripedium guttatum*, EA — *Epipactis atrorubens*, CC — *Cypripedium calceolus*, NO — *Neottia ovata*, PB — *Platanthera bifolia*.

under study occur in mires (*Menyanthoso-sphagnosum*, *Carycoso-sphagnosum* and *Eriophoroso-carycoso-sphagnosum*) and rock habitats with open vegetation. Mires and rock habitats occupy much smaller areas than forests, but are important for conservation, being so-called "hot spots" of orchid diversity in the northern regions.

Three orchid species occur in anthropogenically disturbed areas (Fig. 2). In the study region, this type of habitat is represented by overgrown dumps of gold deposits that were mined in the Yugyd Va National Park from 1982 to 1995 (Poletaeva et al., 2014). In the central and southern parts of distribution ranges, orchid species may also occur in disturbed habitats (Fekete et al., 2019; Djordjević and Tsiftsis, 2020). Helleborines and dactylorrhizas are the most common colonizers of anthropogenic habitats of temperate Europe (Adamowski, 2006). *Epipactis atrorubens*, *E. helleborine*, *Dactylorhiza majalis* and *Malaxis monophyllos* have been reported from transformed habitats in Poland (Jermakowicz et al., 2015; Rewicz et al., 2015, 2016, 2017). The main properties of disturbed habitats that lead to successful orchid colonization include high light availability and diminishing competition (Adamowski, 2006).

Conservation strategies for the areas with relatively intact vegetation, such as the Northern and Subpolar Urals, are focused on the protection of natural habitats and plant communities. At the same time, our results show that for the successful conservation of rare orchid species, it is also important to consider disturbed habitats, many of which are refugia for low-competitive calciphilous species.

Table 2
Result of the modified permutation model envfit.iv applied to NMS ordination.

Factors	Axis 1	Axis 2	r^2	Pr (>r)
F (moisture)	0.41	−0.91	0.67	0.013 *
R (soil acidity)	0.63	0.78	0.68	0.009 **
N (soil nitrogen)	0.34	0.94	0.71	0.002 **
L (illumination)	0.68	−0.74	0.89	0.001 ***

Significance level: * — ($p < 0.05$), ** — ($p < 0.01$), *** — ($p < 0.001$).

4.2. Phytocoenotical preferences and relative niche widths of individual orchid species

Individual orchid species demonstrate different phytocoenotical patterns in the study area (Figs. 2 and 3). *Coeloglossum viride* has the widest range of habitat types among the orchids under study (Fig. 2). According to the literature (Vakhrameeva et al., 2008), this species is not tied to a specific type of plant community across the whole distribution range, and inhabits sites with contrasting environments, from tundra communities in the north to broad-leaved forests in the south (Table 1). *Dactylorhiza fuchsii* and *Gymnadenia conopsea* are other species that have a wide phytocoenotical range (Meekers et al., 2012; Vakhrameeva et al., 2008). *D. fuchsii* occurs in all typical habitat types known from the main species range. *G. conopsea*, across the entire distribution range, occurs in meadows, mires, open woodlands and forest edges, bushes and heaths. In the Urals, the species occurs in a narrower set of potential habitats, growing mostly in water-logged plant communities (mires and forests) and on limestone outcrops (Table 1; Kirillova, 2010). Given the relatively small number of releves (15), we expect that further studies will expand our knowledge on the habitat spectrum of *G. conopsea* in the Urals.

Neottia cordata is a forest species that prefers shaded wet or water-logged spruce forests with a dense moss cover. It can also be found in wet heaths and mires (Delforge, 2006; Vakhrameeva et al., 2008; Kotilínek et al., 2018). Within the study area, *N. cordata* is one of the most common orchid species, which is related to the presence of many suitable habitats. This species occupies similar types of plant communities both in the southern (Tsiftsis et al., 2019) and northern parts of its distribution range (Table 1).

Goodyera repens is another forest orchid species inhabiting all forest formations in the Urals, with a clear preference of plant association *Piceetum myrtilloso-hylocomiosum* (Kirillova et al., 2018). Across the entire distribution range, this species is also a typical spruce forest orchid with a narrow phytocoenotical range. Its successful establishment depends largely on the presence of green moss cover in forest ecosystems (Tsiftsis et al., 2012; Vakhrameeva et al., 2008).

Four orchid species (*Neottia ovata*, *Dactylorhiza maculata*, *D. traunsteineri* and *Corallorrhiza trifida*) are common in mires and water-logged forests within the study area (Fig. 2). Two of these species (*D. maculata* and *D. traunsteineri*) occur in habitats typical of their main ranges (Vakhrameeva, 2000). However, two other species (*N. ovata* and *C. trifida*) occur in fewer potential habitats in northern regions than in the rest of their range.

Dactylorhiza ovata has a wide phytocoenotical range across its entire distribution range. The species can grow in spruce, broad-leaved and mixed forests, forest edges, meadows, mires, grasslands and sand dunes (Vakhrameeva et al., 2008; Kotilínek et al., 2015). In northern regions, *N. ovata* is found in forest and fens, and rarely on the mineral mounds within the sphagnous mires and heathlands (Brzosko and Wróblewska, 2003; Vakhrameeva et al., 2008). In the Urals, the habitat range of the species narrows to forests and mires.

Corallorrhiza trifida is also a species that generally can be found in various plant communities, from tundra to forest-steppe zone (Vakhrameeva et al., 2008). But in the Urals, it can be found only in water-logged mires and forest habitats (Table 1; Fig. 3). We speculate that both *Neottia ovata* and *Corallorrhiza trifida* occupy fewer potential habitats in the Urals because these populations are located at the northern borders of their ranges.

In the study area, *Epipactis atrorubens*, *Cypripedium calceolus* and *Cypripedium guttatum* occur mainly in scarce rock habitats and sloping forest communities (Table 1). These habitats are typical for *E. atrorubens* (Vakhrameeva et al., 1997). At the same time, the *Cypripedium* species can be found in a wider range of the habitat types in other part of their distribution ranges. *C. guttatum* is widespread in broad-leaved and spruce forests, bushes, forest edges, gullies, forested slopes, forest and mountain meadows, water-logged forests, transition mires, limestones and sand screes (Vakhrameeva et al., 2008). *C. calceolus* grows in forests, rarely in forest edges, bushes, mountain meadows and mires (Kull, 1999; Vakhrameeva et al., 2008). In the Northern and Subpolar Urals, the habitat preferences of these species narrow to two vegetation types that occur on limestone bedrock.

Platanthera bifolia is a forest-meadow species without a strict preference for specific plant communities. It can grow in heathlands, forests, heaths, forest edges, meadows and mires (Vakhrameeva et al., 2008). In our study, only single habitats are found in the Northern Urals (Table 1), which may be the northern edge of the species' distribution range.

A comparative analysis of phytocoenotic confinements of the orchids in the study area and within the entire distribution range has allowed us to distinguish two groups of species with different habitat preferences. The first group includes the species for which the phytocenotic amplitude narrows in the north compared with the main part of their ranges. These species include *Gymnadenia conopsea*, *Neottia ovata*, *Corallorhiza trifida*, *Cypripedium calceolus*, *C. guttatum* and *Platanthera bifolia*. In the study area, most of them are found in habitats with substrate enriched by calcium, i.e., fertile mineral fens and limestones. Previous studies have reported a wider spectrum of plant communities for these species, including various forests, mires, meadows and bushes (Kull, 1999; Meekers et al., 2012; Vakhrameeva et al., 2008; Kotilínek et al., 2015). In other words, near the distribution limits, these species become more demanding of the quality of the substrate and have a higher level of specialization than in the centers of the species ranges. This conclusion is consistent with previous studies that have highlighted carbonate soils as important for the growth and development of orchids (Tsiftsis et al., 2008; Landi et al., 2009; Leuschner and Ellenberg, 2017; Procházka et al., 2017; Djordjevic and Tsiftsis, 2019).

The second group (*Coeloglossum viride*, *Dactylorhiza* species, *Goodyera repens*, *Neottia cordata* and *Epipactis atrorubens*) includes orchid species whose phytocoenotical preferences do not narrow in the northern areas compared to the main part of their distribution ranges. These species are located in areas with conditions more favorable for population stability than the species that change their habitat spectrum in the study area.

4.3. Distribution of orchid habitats across ecological gradients

NMS ordination has shown that light and soil nitrogen are the main ecological drivers of orchid distribution across the vegetation types in the Urals (Fig. 4). The importance of light regime is confirmed by data obtained from other studies (Abernethy, 2002; Diez and Pulliam, 2007; Lõhmus and Kull, 2011; Djordjević et al., 2016b; Djordjević and Tsiftsis, 2020). Light availability is considered to be the main factor that limits the diversity and structure of temperate and boreal forest low layers (Barbier et al., 2008). Light is also crucial for orchid demography (Shefferson et al., 2006; Jacquemyn et al., 2010a, b; Hurskainen et al., 2017). High light availability is known to have a positive effect on the reproductive success of several orchids (Kirillova and Kirillov, 2019, 2020).

Habitats of *Goodyera repens, Neottia cordata* and *Cypripedium guttatum* are represented mainly by shaded forest communities. The first two species are well known habitat specialists across their entire ranges (Delforge, 2006; Vakhrameeva et al., 2008; Kotilínek et al., 2018; Tsiftsis et al., 2012, 2019). Surprisingly, the habitat illumination preferences of *C. guttatum*

narrows in the Urals. In other parts of the range, this species is common both in shaded forests and open treeless plant communities, e.g., meadows, mires and even screes (Vakhrameeva et al., 2008; Kirillov and Kirillova, 2019). Moreover, *C. guttatum* showed the narrowest relative niche width among the orchids studied (Fig. 3). We speculate that such a reduction in the ecological and phytocoenotical amplitude of this species is due to the northern location of the population.

NMS ordination indicated that releves with *Dactylorhiza* species occur in regions with the highest light conditions. In the study area, *D. maculata*, *D. traunsteineri* and *D. fuchsii* have different phytocoenotic preferences (Fig. 2) and niche widths (Fig. 3), but nevertheless prefer open plant communities. Soil fertility is the main distinguishing factor for these species (Fig. 4). *D. maculata* habitats are located in unfertile conditions along soil nitrogen and acidity gradients. *D. traunsteineri* and *D. fuchsii* establish habitats with more nutrient soils. Ståhlberg (2009) reported similar results and found *D. maculata* to prefer more acid soils than *D. fuchsii* in Scandinavia. Soil characteristics are considered important factors that affect the distribution and abundance of orchid species (Rasmussen, 1995; Stuckey, 1967; Tsiftsis et al., 2008). Moreover, soil acidity is a crucial factor that distinguishes the habitats of closely related species (Djordjević and Tsiftsis, 2020).

Thus, according to the ecological parameters of habitats, some of the studied orchid species can be classified as habitat specialists with relatively narrow ecological confinement in the Urals. These species include *Goodyera repens*, *Cypripedium guttatum* and *Dactylorhiza maculata*. *Neottia cordata* and *D. fuchsii* are the examples of species that grow under diverse ecological parameters.

5. Conclusions

In general, our research has revealed that the Pechoro-Ilychsky Reserve and Yugyd Va National Park provide suitable conditions for many orchid species that prefer forest ecosystems. The system of protected areas, located in the Urals, is aimed primarily at protecting undisturbed forests. Thus, Ural populations of forest orchids (*Goodyera repens* and *Neottia cordata*) and orchid species with wide habitat and ecological ranges (*Dactylorhiza fuchsii* and *Coeloglossum viride*) may continue to be relatively stable during global climate change. However, to preserve orchid species with high levels of habitat specialization (*Cypripedium guttatum*, *Epipactis atrorubens*), conservation practices should pay a special attention to the protection of marginal habitats, i.e., limestones and rich fens. Another important issue is that several orchids consistently occur in plots located in areas disturbed by anthropogenic activity. In our case, this type of habitat is represented mainly by abandoned gold mines and overgrown roads. These findings indicate that reduced competition from other plants has a direct beneficial effect on the development of several orchid populations (most notably *Cypripedium calceolus*). Thus, the presence of such habitats must be considered when carrying out future conservation measures.

Author contributions

IA, YA conceived the idea. IA, YA, SV donated the data. IA, YA, AB analyzed the data. IA and YA wrote the manuscript; other authors provided editorial advice.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2022.08.005.

References

Abernethy, A., 2002. Light Regimes as a Control of Terrestrial Orchid Distribution in New Zealand. Dissertation, University of Canterbury.

Adamowski, W., 2006. Expansion of native orchids in anthropogenous habitats. Pol. Bot. Stud. 22, 35—44.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved — a critical review for temperate and boreal forests. For. Ecol. Manage. 254, 1—15. https://doi.org/10.1016/j.foreco.2007.09.038.

Brzosko, E., Wróblewska, A., 2003. Low allozymic variation in two island populations of *Listera ovata* (Orchidaceae) from NE **Poland**. Ann. Bot. Fenn. 40, 309—315.

Cîşlariu, A.G., Mânzu, C.C., Baltag, E.Ş., 2021. Which are the drivers that influence the performance of *Ligularia sibirica* populations from Romania? Plant Biosyst. 155, 394—405. https://doi.org/10.1080/11263504.2020.1756972.

Delforge, P., 2006. Orchids of Europe, North Africa and the Middle East. A and C Black, London.

Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology — a review. Basic Appl. Ecol. 4, 493—506. https://doi.org/10.1078/1439-1791—00185.

Diez, J.M., Pulliam, H.R., 2007. Hierarchical analysis of species distribution and abundance across environmental gradients. Ecology 88, 3144—3152. https://doi.org/10.1890/07-0047.1.

Djordjević, V., Tsiftsis, S., 2019. Patterns of orchid species richness and composition in relation to geological substrates. Wulfenia 26, 1—21.

Djordjević, V., Tsiftsis, S., 2020. The role of ecological factors in distribution and abundance of terrestrial orchids. In: Mérillon, J.—M., Kodja, H. (Eds.), Orchids phytochemistry, Biology and Horticulture. Springer Nature Switzerland AG, pp. 1—71. https://doi.org/10.1007/978-3-030-11257-8_4-1.

Djordjević, V., Tsiftsis, S., Lakušić, D., et al., 2016a. Factors affecting the distribution and abundance of orchids in grasslands and herbaceous wetlands. Syst. Biodivers. 14, 355—370. https://doi.org/10.1080/14772000.2016.1151468.

Djordjević, V., Tsiftsis, S., Lakušić, D., et al., 2016b. Niche analysis of orchids of serpentine and non—serpentine areas: implications for conservation. Plant Biosyst. 150, 710—719. https://doi.org/10.1080/11263504.2014.990534.

Djordjević, V., Tsiftsis, S., Lakušić, D., et al., 2020a. Orchid species richness and composition in relation to vegetation types. Wulfenia 27, 183—210.

Djordjević, V., Tsiftsis, S., Lakušić, D., et al., 2020b. Patterns of distribution, abundance and composition of forest terrestrial orchids. Biodivers. Conserv. 29, 4111—4134. https://doi.org/10.1007/s10531-020-02067-6.

Ellenberg, H., Weber, H.E., Dull, R., et al., 1992. Zeigerwerte von Pflanzen in mitteleuropa. Scr. Geobot. 18, 1—248.

Fay, M.F., 2018. Orchid conservation: how can we meet the challenges in the twenty—first century? Bot. Stud. 59, 1—6. https://doi.org/10.1186/s40529-018-0232-z.

Fay, M.F., Pailler, T., Dixon, K.W., 2015. Orchid conservation: making the links. Ann. Bot. 116, 377—379. https://doi.org/10.1093/aob/mcv142.

Fekete, R., Löki, V., Urgyán, R., et al., 2019. Roadside verges and cemeteries: comparative analysis of anthropogenic orchid habitats in the Eastern Mediterranean. Ecol. Evol. 9, 6655—6664. https://doi.org/10.1002/ece3.5245.

Fomin, V.V., Zalesov, S.V., Popov, A.S., et al., 2017. Historical avenues of research in Russian forest typology: ecological, phytocenotic, genetic, and dynamic classifications. Can. J. For. Res. 47, 849—860. https://doi.org/10.1139/cjfr-2017-0011.

Fridley, J.D., Vandermast, D.B., Kuppinger, D.M., et al., 2007. Co-occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. J. Ecol. 95, 707—722. https://doi.org/10.1111/j.1365-2745.2007.01236.x.

Gale, S.W., Fischer, G.A., Cribb, P.J., et al., 2018. Orchid conservation: bridging the gap between science and practice. Bot. J. Linn. Soc. 186, 425—434. https://doi.org/10.1093/botlinnean/boy003.

Ghorbani, A., Gravendeel, B., Naghibi, F., et al., 2014. Wild orchid tuber collection in Iran: a wake—up call for conservation. Biodivers. Conserv. 23, 2749—2760. https://doi.org/10.1007/s10531-014-0746-y.

Hurskainen, S., Jäkäläniemi, A., Ramula, S., et al., 2017. Tree removal as a management strategy for the lady's slipper orchid, a flagship species for herb-rich forest conservation. For. Ecol. Manag. 406, 12—18. https://doi.org/10.1016/j.foreco.2017.09.056.

Ipatov, V.S., Mirin, D.M., 2008. Description of Phythocoenosis. Methodical Recommendations. St. Petersburg State University press, St. Petersburg.

Jacquemyn, H., Brys, R., Jongejans, E., 2010a. Size-dependent flowering and costs of reproduction affect population dynamics in a tuberous perennial woodland orchid. J. Ecol. 98, 1204–1215. https://doi.org/10.1111/j.1365-2745.2010.01697.x.

Jacquemyn, H., Brys, R., Jongejans, E., 2010b. Seed limitation restricts population growth in shaded populations of a perennial woodland orchid. Ecology 91, 119–129. https://doi.org/10.1890/08-2321.1.

Jermakowicz, E., Ostrowiecka, B., Tałałaj, I., et al., 2015. Male and female reproductive success in natural and anthropogenic populations of *Malaxis monophyllos* (L.) Sw. (Orchidacea). Biodivers. Res. Conserv. 39, 37–44. https://doi.org/10.1515/biorc-2015-0024.

Jersáková, J., Malinová, T., Jeřábková, K., et al., 2011. Biological flora of the British isles: *Pseudorchis albida* (L.) Á. and D. Löve. J. Ecol. 99, 1282–1298. https://doi.org/10.1111/j.1365-2745.2011.01868.x.

Jersáková, J., Traxmandlová, I., Ipser, Z., et al., 2015. Biological flora of central Europe: *Dactylorhiza sambucina* (L.) soó. Perspect. Plant Ecol. 17, 318–329. https://doi.org/10.1016/j.ppees.2015.04.002.

Kirillov, D., Kirillova, I., 2019. *Cypripedium guttatum* Sw. Occurrence dataset. In: The Komi Republic. Institute of Biology of Komi Scientific Centre of the Ural Branch of the Russian Academy of Sciences. https://doi.org/10.15468/pdjzui. accessed via GBIF.org on 2019–03–27.

Kirillova, I.A., 2010. Orchids of the Pechora-Ilych Reserve (Northen Urals). Institute of Biology of KSC UB RAS, Syktyvkar. https://doi.org/10.13140/2.1.3841.1848.

Kirillova, I.A., 2015. Orchids of Subpolar Urals: features of biology and structure of populations. Proceedings of the Komi Science Centre of the Ural Division of the Russian Academy of Sciences 1, 48–54.

Kirillova, I.A., Kirillov, D.V., 2019. Effect of lighting conditions on the reproductive success of *Cypripedium calceolus* L. (Orchidacea, Liliopsida). Biol. Bull. 46, 1317–1324. https://doi.org/10.1134/S1062359019100157.

Kirillova, I.A., Kirillov, D.V., 2020. Effect of illumination conditions on the reproductive success of *Epipactis helleborine* (L.) Crantz (Orchidaceae). Russ. J. Ecol. 51, 389–393. https://doi.org/10.1134/S1067413620040098.

Kirillova, I.A., Kirillov, D.V., 2021. Population dynamics, reproductive success, and seasonal development of *Cypripedium calceolus* under different growing conditions as a response to weather factors. Contemp. Probl. Ecol. 14, 472–482. https://doi.org/10.1134/S1995425521050061.

Kirillova, I.A., Degteva, S.V., Dubrovskiy, Y.A., et al., 2018. Ecology and structure of *Goodyera repens* (L.) R. Br. (Orchidacea) coenopopulations in the northern Urals. Theoretic. Appl. Ecol. 3, 69–77. https://doi.org/10.25750/1995-4301-2018-3-069-077.

Kornienko, E.V., 2011. Atlas of the Komi Republic. Feorya, Moscow.

Kotilínek, M., Tatarenko, I., Jersáková, J., 2018. Biological flora of the British isles: *Neottia cordata*. J. Ecol. 106, 444–460.

Kotilínek, M., Těšitelová, T., Jersáková, J., 2015. Biological flora of the British isles: *Neottia ovata*. J. Ecol. 103, 1354–1366. https://doi.org/10.1111/1365-2745.12444.

Kühn, R., Pedersen, H., Cribb, P., 2019. Field Guide to the Orchids of Europe and the Mediterranean. Royal Botanic Gardens.

Kull, T., 1999. *Cypripedium calceolus* L. J. Ecol. 87, 913–924.

Kull, T., Hutchings, M.J., 2006. A comparative analysis of decline in the distribution ranges of orchid species in Estonia and the United Kingdom. Biol. Conserv. 129, 31–39. https://doi.org/10.1016/j.biocon.2005.09.046.

Landi, M., Frignani, F., Lazzeri, C., et al., 2009. Abundance of orchids on calcareous grasslands in relation to community species, environmental, and vegetation conditions. Russ. J. Ecol. 40, 486–494. https://doi.org/10.1134/S1067413609070066.

Lavorel, S., Grigulis, K., McIntyre, S., et al., 2008. Assessing functional diversity in the field — methodology matters. Funct. Ecol. 22, 134–147. https://doi.org/10.1111/j.1365-2435.2007.01339.x.

Leuschner, C., Ellenberg, H., 2017. Ecology of central European non-forest vegetation: coastal to alpine, Natural to Man-Made Habitats: Vegetation Ecology of Central Europe, 2. Springer, Cham.

Liu, Q., Chen, J., Corlett, R.T., et al., 2015. Orchid conservation in the biodiversity hotspot of southwestern China. Conserv. Biol. 29, 1563–1572. https://doi.org/10.1111/cobi.12584.

Lõhmus, A., Kull, T., 2011. Orchid abundance in hemiboreal forests: stand-scale effects of clearcutting, green-tree retention, and artificial drainage. Can. J. For. Res. 41, 1352–1358. https://doi.org/10.1139/x11-047.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253. https://doi.org/10.1038/35012251.

Meekers, T., Hutchings, M.J., Honnay, O., et al., 2012. Biological flora of the British Isles: *Gymnadenia conopsea* s.l. J. Ecol. 100, 1269–1288. https://doi.org/10.1111/j.1365-2745.2012.02006.x.

Neshataev, V.Yu., 2001. The project of All-Russian code of phytocoenological nomenclature. Vegetation of Russia 1, 62–70. https://doi.org/10.31111/vegrus/2001.01.62.

Oksanen, J., Blanchet, G.F., Friendly, M., et al., 2018. vegan: Community Ecology Package. R package version 2.5-3. https://CRAN.R-project.org/package=vegan.

Ozinga, W.A., Colles, A., Bartish, I.V., et al., 2013. Specialists leave fewer descendants within a region than generalists. Global Ecol. Biogeogr. 22, 213–222. https://doi.org/10.1111/j.1466-8238.2012.00792.x.

Plotnikova, I.A., Degteva, S.V., Dubrovskiy, YuA., 2010. Ecology and structure of coenopopulations of *Coeloglossum viride* (Orchidaceae) in the nothern Urals. Rastit. Resur. 4, 35–47.

Pohjanmies, T., Genikova, N., Hotanen, J.P., et al., 2021. Site types revisited: comparison of traditional Russian and Finnish classification systems for European boreal forests. Appl. Veg. Sci. 24, e12525. https://doi.org/10.1111/avsc.12525.

Poletaeva, I.I., Degteva, S.V., Kirillova, I.A., 2014. The cenopopulation characteristics of some rare plants in the gold mine dumps (Subpolar Urals). Rastit. Resur. 50, 53–66.

Procházka, A., Mikita, T., Jelínek, P., 2017. The relationship between some forest stand properties and the occurrence of orchids in the central part of the Moravian Karst Protected Landscape Area. Acta Univ. Silvic. Mendel. Brun. 65, 919–931. https://doi.org/10.11118/actaun201765030919.

Rasmussen, H., 1995. Terrestrial Orchids from Seed to Mycotrophic Plant. Cambridge University Press, Cambridge.

Rewicz, A., Zielińska, K.M., Kiedrzyński, M., et al., 2015. Orchidaceae in the anthropogenic landscape of Central Poland: diversity, extinction and conservation perspectives. Arch. Biol. Sci. 67, 119–130. https://doi.org/10.2298/ABS140428014R.

Rewicz, A., Kolodziejek, J., Jakubska-Busse, A., 2016. The role of anthropogenic habitats as substitutes for natural habitats: a case study on *Epipactis helleborine* (L.) Crantz (Orchidaceae, Neottieae). Variations in size and nutrient composition of seeds. Turk. J. Bot. 40, 258–268. https://doi.org/10.3906/bot-1404-69.

Rewicz, A., Jaskuła, R., Rewicz, T., et al., 2017. Pollinator diversity and reproductive success of *Epipactis helleborine* (L.) Crantz (Orchidaceae) in anthropogenic and natural habitats. PeerJ 5, 3159. https://doi.org/10.7717/peerj.3159.

Sagarin, R.D., Gaines, S.D., 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? Ecol. Lett. 5, 137–147. https://doi.org/10.1046/j.1461-0248.2002.00297.x.

Schödelbauerová, I., Roberts, D.L., Kindlmann, P., 2009. Size of protected areas is the main determinant of species diversity in orchids. Biol. Conserv. 142, 2329–2334. https://doi.org/10.1016/j.biocon.2009.05.015.

Shefferson, R.P., Kull, T., Tali, K., 2006. Demographic response to shading and defoliation in two woodland orchids. Folia Geobot. 41, 95–106. https://doi.org/10.1007/BF02805264.

Sizonenko, T.A., Dubrovskiy, Y.A., Novakovskiy, A.B., 2020. Changes in mycorrhizal status and type in plant communities along altitudinal and ecological gradients — a case study from the Northern Urals (Russia). Mycorrhiza 30, 445–454. https://doi.org/10.1007/s00572-020-00961-z.

Skovsgaard, J.P., Vanclay, J.K., 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. Forestry 81, 13–31. https://doi.org/10.1093/fores try/cpm041.

Ståhlberg, D., 2009. Habitat differentiation, hybridization and gene flow patterns in mixed populations of diploid and autotetraploid *Dactylorhiza maculata* s.l. (Orchidaceae). Evol. Ecol. 23, 295–328. https://doi.org/10.1007/s10682-007-9228-y.

Štípková, Z., Kindlmann, P., 2021. Orchid extinction over the last 150 years in the Czech Republic. Diversity 13, 78. https://doi.org/10.3390/d13020078.

Stuckey, I., 1967. Environmental factors and the growth of native orchids. Am. J. Bot. 54, 232–241. https://doi.org/10.1002/j.1537-2197.1967.tb06914.x.

Swarts, N.D., Dixon, K.W., 2009. Terrestrial orchid conservation in the age of extinction. Ann. Bot. 104, 543–556. https://doi.org/10.1093/aob/mcp025.

Taskaev, A.I., 2006. Virgin Forests of Komi: the UNESCO World Cultural and Natural Heritage Site. Publishing Centre Design, Information, Cartography, Moscow.

Tsiftsis, S., Antonopoulos, Z., 2017. Atlas of the Greek Orchids, I. Mediterraneo Editions, Rethymno.

Tsiftsis, S., Djordjević, V., Tsiripidis, I., 2019. *Neottia cordata* (Orchidaceae) at its southernmost distribution border in Europe: threat status and effectiveness of Natura 2000 Network for its conservation. J. Nat. Conserv. 48, 27–35. https://doi.org/10.1016/j.jnc.2019.01.006.

Tsiftsis, S., Tsiripidis, I., Papaioannou, A., 2012. Ecology of the orchid *Goodyera repens* in its southern distribution limits. Plant Biosyst. 146, 857–866. https://doi.org/10.1080/11263504.2011.642416.

Tsiftsis, S., Tsiripidis, I., Karagiannakidou, V., et al., 2008. Niche analysis and conservation of the orchids of east Macedonia (NE Greece). Acta Oecol. 33, 27–35. https://doi.org/10.1016/j.actao.2007.08.001.

Vakhrameeva, M.G., 2000. In: Pavlov, V.N. (Ed.), Biological Flora of the Moscow Region, part 14, Genus Dactylorhiza. Grif and K, Moscow, pp. 55–86.

Vakhrameeva, M.G., Tatarenko, I.V., Varlygina, T.I., et al., 2008. Orchids of Russia and Adjacent Countries (Within the Borders of the Former USSR). A.R.G. Gantner Verlag, Ruggell.

Vakhrameeva, M.G., Varlygina, T.I., Tatarenko, I.V., 2014. Orchids of Russia (Biology, Ecology and Protection). KMK Scientific Press Ltd., Moscow.

Vakhrameeva, M.G., Varlygina, T.I., Batalov, A.E., et al., 1997. In: Pavlov, V.N., Tikhomirov, V.N. (Eds.), Biological Flora of the Moscow Region, part 13, Genus Epipactis. Poliex, Moscow, pp. 50–87.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, fourth ed. Springer, New York.

Vogt-Schilb, H., Munoz, F., Richard, F., et al., 2015. Recent declines and range changes of orchids in Western Europe (France, Belgium and Luxembourg). Biol. Conserv. 190, 133–141. https://doi.org/10.1016/j.biocon.2015.05.002.

Wraith, J., Pickering, C., 2018. Quantifying anthropogenic threats to orchids using the IUCN Red List. Ambio 47, 307–317. https://doi.org/10.1007/s13280-017-0964-0.

Wraith, J., Pickering, C., 2019. A continental scale analysis of threats to orchids. Biol. Conserv. 234, 7–17. https://doi.org/10.1016/j.biocon.2019.03.015.

Zelený, D., Schaffers, A.P., 2012. Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. J. Veg. Sci. 23, 419–431. https://doi.org/10.1111/j.1654-1103.2011.01366.x.

Zhou, Z., Shi, R., Zhang, Y., et al., 2021. Orchid conservation in China from 2000 to 2020: achievements and perspectives. Plant Divers. 43, 343–349. https://doi.org/10.1016/j.pld.2021.06.003.