



# Impacts of introduced dwarf pine (*Pinus mugo*) on the diversity and composition of alpine vegetation

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**Abstract:** Dwarf pine (*Pinus mugo*) is a successful pioneer tree, but also an invader of the subalpine belt in Central-European mountains. In the Hrubý Jeseník Mts. (Czech Republic), dwarf pine was introduced at the end of the 19th century by humans into alpine communities. To analyse the influence of non-native woody species on species diversity, vegetation composition and the ecological bioindication of invaded alpine communities, three habitats (non-invaded alpine grasslands, gaps of alpine grasslands within dwarf pine stands and closed dwarf pine stands) were compared at two localities (Keprník, Tabulové kameny) using the space-for-time substitution approach. Plant species composition was assessed by means of phytosociological relevés, and bioindication by means of Ellenberg indicator values. At both localities, both beta and gamma diversity were lower, and species composition more uniform in dwarf pine plantations in contrast to the gaps within and alpine grasslands outside of dwarf pine stands. At Keprník, alpha diversity was lower in the dwarf-pine plantation than outside of it, while at Tabulové kameny no significant differences were found. This is probably due to the somewhat different spatial structure of the dwarf pine stands and the different timing of dwarf pine introduction at these localities. Bioindication showed that dwarf-pine stands were drier, more shaded and had a higher soil fertility than alpine grasslands. Dwarf pine colonisation of alpine grasslands causes the extinction of many endangered plant species, complicating conservation goals. Because of the limited size of alpine areas, changes caused by dwarf pine in medium-high mountains might be more significant than in mountains with large alpine forest-free areas.

**Nomenclature:** For vascular taxa Kubát et al. (2002), for mosses Hill et al. (2006), for lichens Neuhäuslová and Kolbek (1982).

## Introduction

Dwarf pine (*Pinus mugo*) creates compact shrubby poly-commons forming an interjacent belt between montane coniferous forest and alpine forest-free areas in Central European mountains (Jirásek 1996a, Richardson and Rundel 1998). While dwarf pine creates a continuous “krummholz” belt in the subalpine region of high European mountains (e.g., the Alps, Carpathians), only small dwarf pine belts are naturally developed in several medium-high mountains of Central Europe (Ellenberg 1988). In other medium-high mountains, dwarf pine occurs merely in plantations.

In the Hercynian mountain region (*sensu* Jeník 1998), dwarf pine is part of the natural vegetation only above the treeline (1200–1450 m a.s.l.) in the Giant Mountains (Štursa 1966, Skalický 1988). In the Hrubý Jeseník Mountains, the alpine treeline was formed by spruce (*Picea abies*) clumps (Jeník and Hampel 1992, Treml and Banaš 2008). The historical absence of dwarf pine in the subalpine and alpine zone of Hrubý Jeseník Mts. was probably associated with specific postglacial immigration (Skalický 1988, Jeník and Hampel 1992, Rybníček and Rybníčková 2004). Hence, unique ecological conditions were formed in the treeline ecotone and

alpine zone of these mountains (Jeník 1961, Klimeš and Klimešová 1991).

Dwarf pine is well known to be a successful pioneer tree in naturally disturbed sites or fallow pastures of subalpine regions, and is an effective invader of new habitats outside its natural range (Dullinger et al. 2003). Several recent papers show that the presence of dwarf pine significantly modifies some environmental factors in the subalpine zone of mountains with small alpine areas in Central Europe. Dwarf pine plantations influence microclimatic as well as soil conditions, including the thickness of soil organic layers, their acidity and nutrient content, as was documented from the Giant Mts. (Soukupová et al. 2001a, Svoboda 2001, Treml and Křížek 2006, Treml et al. 2010a). Soukupová et al. (2001a, b) also observed changes in biomass production, edge effect formation, decrease in vegetation diversity and alteration of species composition as a consequence of dwarf pine planting in the Giant Mts. In the Hrubý Jeseník Mts., dwarf pine was first planted in the subalpine and alpine zone in the late 19<sup>th</sup> century (Hošek 1964, Jeník and Hampel 1992) and has since then been expanding to relict habitats (Treml et al. 2010b), including alpine grasslands and also sparse spruce (*Picea abies*) and juniper clumps near the alpine treeline (Zeidler et

al. 2009). Dwarf pine is thus a relatively new element in the local alpine vegetation, which offers us the opportunity to study the reaction of indigenous vegetation to this introduced tree species. This has also important consequences for nature conservation, since the small area and geographical isolation of the alpine vegetation in the Hrubý Jeseník Mts. (Klimeš and Klimešová 1991, Treml et al. 2010b) result in a low probability of plant species (re-)colonisation (MacArthur and Wilson 1967). Thus, the spread of dwarf pine may cause a direct threat to the presently rare alpine communities (Kočí 2007a).

In this paper we asked the following questions: (1) What are the changes in species diversity and composition of alpine vegetation due to the planting and expansion of dwarf pine? (2) Are there any shifts in ecological conditions of the invaded stands based on bioindication?

## Materials and methods

### Study sites

This research was performed at two localities in the highest ridge areas of the Hrubý Jeseník Mountains (Czech Republic) at 12 km apart (Fig. 1). The first is Tabulové kameny (50°5'15.398"N, 17°13'52.435"E) west of the Praděd peak. The other locality is an area north-east of the Keprník peak (50°10'35.601"N, 17°6'6.909"E). Dwarf pine was planted there in around 1880 at Keprník and in 1900 at Tabulové kameny (Hošek 1964, Jeník and Hampel 1992).

The area of Tabulové kameny is formed by gneisses and slates, and the surface shows numerous periglacial elements, mainly cryoplanation terraces and thufurs (Treml et al.

2010a). The warmest month is July (average temperature 9.7 °C) and the coldest is January (average temperature -7.5 °C). The mean annual precipitation is 1213 mm (Lednický 1985). The area of Keprník is formed by mica schist, and its surface displays periglacial elements similar to that at Tabulové kameny. Soils are mainly sandy-loamy and classified as Haplic Cambisols (Treml et al. 2010a). The climate is very similar to that of Tabulové kameny.

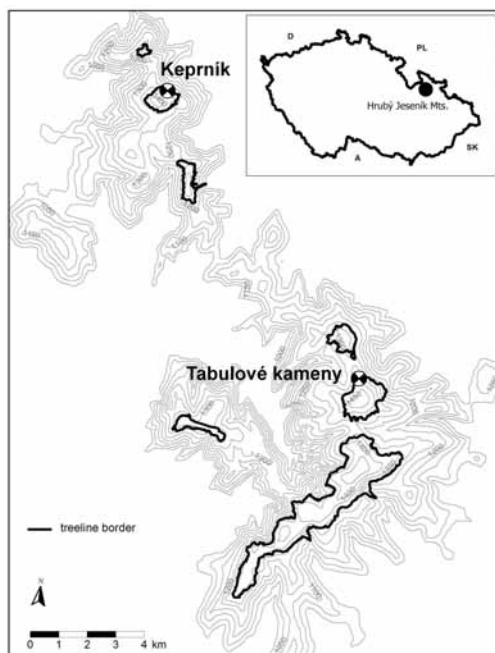
Both localities are covered by wind-swept alpine grasslands of the alliance *Juncion trifidi* Krajina 1933 (association *Cetrario-Festucetum supinae* Jeník 1961), closed alpine grasslands of the alliance *Nardo strictae-Caricion bigelowii* Nordhagen 1943 (association *Carici bigelowii-Nardetum strictae* (Zlatník 1928) Jeník 1961) and 90–110 year old secondary (planted) dwarf pine stands of the alliance *Pinion mughii* Pawłowski in Pawłowski et al. 1928 (association *Myrtillo-Pinetum mughii* Hadač 1956) (see Jirásek 1996a, Kočí 2007a).

At the sites where dwarf pine was introduced, the localities significantly differ in alpine grassland habitat conditions (Table 1). Alpine grasslands at Tabulové kameny occur at higher altitudes and have a lower demand for light and higher demand for moisture and soil reaction than the alpine grasslands at Keprník.

### Sampling

To reveal patterns of community change through time due to plantation of dwarf pine, we used the space-for-time substitution method (Pickett 1989). At each locality, a 2 ha area was selected including a large closed dwarf pine stand (plantations) in its centre surrounded by alpine grasslands. Three habitats were sampled at each locality: (i) closed stands of planted *Pinus mugo* (further: dwarf pine), (ii) unshaded stands of alpine grasslands surrounded by dwarf pine stands (gaps), and (iii) stands of alpine grassland vegetation outside of closed stands of dwarf pine (alpine grasslands). Alpine grasslands were sampled in sufficient distance from closed dwarf pine stands to ensure that the edge effect of dwarf pine stands did not influence the composition of sampled vegetation and the samples were not too distant from closed dwarf pine stands (10 m < distance < 50 m). All gaps with an area exceeding 4 m<sup>2</sup> were sampled within dwarf pine stands, whereby the plots were situated in the centre of each gap. The gaps represent remnants of alpine grasslands surrounded by spreading dwarf pine and not gaps created by decay of dwarf pine stands. Twenty plots per dwarf pine stands and alpine grasslands were haphazardly selected at each locality, resulting in 80 plots at both localities (2 habitats × 2 localities × 20 plots), while a total of 101 plots of gaps were sampled at the localities (50 plots at Keprník and 51 plots at Tabulové kameny). Plots were 2 m × 2 m in size.

The plots of the compared habitats did not differ significantly in geomorphological parameters between the sites studied (aspect, slope; Watson-Williams test and two sample t-test; all  $P > 0.15$ ). Field data were collected from July 25 to August 28, 2007.



**Figure 1.** Map of the Hrubý Jeseník Mts. with the two study localities (Tabulové kameny, Keprník).

**Table 1.** Comparison of environmental variables (altitude, slope, aspect) and Ellenberg indicator values based on floristic composition of alpine grasslands at the two localities studied (Keprník, Tabulové kameny). Differences in aspect between localities were tested by the Watson-Williams test ( $F^*$ ); otherwise a two sample t-test was used (t).

Variable	Keprník		Tabulové kameny		P
	$\bar{x} \pm$	s.e.	$\bar{x} \pm$	s.e.	
Altitude (m a.s.l.)	1419±	1	1462±	1	<0.001
Slope ( $^\circ$ )	9.5±	0.8	9.9±	1.8	0.573
Aspect ( $^\circ$ )	1.6±	5.8	340.2±	5.8	0.005*
Light	6.3±	0.1	6.0±	0.1	0.023
Temperature	1.9±	0.1	2.0±	0.1	0.314
Moisture	3.4±	0.2	4.0±	0.1	<0.001
Soil reaction	2.2±	0.1	2.6±	0.1	0.005
Nitrogen	2.2±	0.1	2.2±	0.1	0.430

Plant species composition was assessed by means of phytosociological relevés. Species cover was estimated using Braun-Blanquet's seven-grade abundance-dominance scale (Kent and Coker 1992).

#### Data analysis

Endangered species of the IUCN categories CR, EN, VU, LR and DD were selected from the Red list of vascular plants of the Czech Republic (Procházka 2001). To avoid possible bias in calculating diversity because of the different number of sampled plots per habitat, the number of plots of gaps was decreased using a random plot selection, resulting in 20 plots per habitat/locality. Species richness (alpha diversity) was expressed as the number of either all or only endangered species per plot, excluding dwarf pine. We used the Sørensen index of dissimilarity (Koleff et al. 2003) as a measure of beta diversity, and calculated it separately for each pair of plots in each habitat and locality. Gamma diversity was expressed as the sum of either all or only endangered species over twenty plots sampled in each habitat and locality. Ellenberg values (Ellenberg et al. 1992) function well as surrogates for changes in environmental factors associated with plant communities (van der Maarel 1993). For each plot, the means of Ellenberg indicator values of vascular plants for moisture, light, temperature, soil reaction and nitrogen (Ellenberg et al. 1992) were calculated without species weighting. Dwarf pine was excluded from these calculations.

Differences in species richness of all species and Ellenberg indicator values were analysed by general linear models, whereas post hoc comparisons on cell means were conducted using Fisher's LSD test. In the case of alpha diversity of endangered species, generalised linear models with Poisson distributions of the dependent variable and log link function were used. In all analyses, localities (Tabulové kameny, Keprník) and habitats (dwarf pine, gaps, alpine grasslands) were used as fixed, crossed factors. The bootstrap mean and its 95% confidence interval (from 200 bootstrap samples) were calculated for all dissimilarity coefficients (beta diver-

sity measure) among samples of each group. Statistical analyses were carried out in JUICE 7.0 (Tichý 2002) and Statistica 10 (Statsoft Inc.).

The floristic composition was analysed using CANOCO 4.5 software (ter Braak and Šmilauer 2002). We used detrended correspondence analysis (DCA) to characterise the general pattern in species composition variation over habitats and localities. Ellenberg indicator values were passively projected onto the ordination diagram. Subsequently, the effect of dwarf pine planting on the species composition of dwarf pine plantations, gaps and alpine grasslands was tested using partial canonical correspondence analysis (pCCA) with Monte Carlo permutation tests (999 permutations; Lepš and Šmilauer 2003). Localities were used as blocks in the analysis. Species were separated into diagnostic and common based on a fidelity analysis using *phi*-coefficient (Chytrý et al. 2002) in the software JUICE 7.0 (Tichý 2002). Species with a *phi*-coefficient higher than 0.20 were considered to be diagnostic of a particular habitat.

## Results

#### Species diversity and composition

No difference in cover of dwarf pine in dwarf pine stands was found between the localities (Tabulové kameny: mean  $\pm$  s.e.  $85 \pm 9\%$ , Keprník:  $80 \pm 12\%$ , two-sample t-test,  $P = 0.121$ ). No difference in gap size between localities was found (mean  $\pm$  s.e.; Keprník:  $58.8 \pm 10.3 \text{ m}^2$ , Tabulové kameny:  $52.1 \pm 6.6 \text{ m}^2$ ; two sample t-test,  $P = 0.583$ ). Comparing equal-sized data sets, remarkable differences in all diversity measures were found (Table 2). Alpha diversity significantly differed between localities ( $P < 0.001$ ) and habitats ( $P < 0.001$ ). There was also a significant effect of locality  $\times$  habitat interaction ( $P < 0.001$ ). While no differences in alpha diversity of alpine grasslands were observed between localities, alpha diversity of dwarf pine stands and gaps was significantly lower than that of alpine grasslands at Keprník, but not at Tabulové kameny (Table 2). At both localities, significantly lower values of beta diversity were found in dwarf pine stands than in the other two habitats. The beta diversity values also showed that stands at Keprník are generally more heterogeneous than those at Tabulové Kameny. The gamma diversity was highest in the alpine grasslands, followed by the gaps, with the lowest value in the dwarf pine stands at both localities.

Analysing endangered species, a significantly lower alpha diversity was found in dwarf pine stands in comparison with gaps and alpine grasslands (locality:  $P = 0.083$ ; habitat:  $P < 0.001$ ; locality  $\times$  habitat:  $P = 0.233$ ). The gamma diversity of endangered species was highest in the alpine grasslands, followed by the gaps, with the lowest value found for the dwarf pine stands at both localities (Table 2). Many endangered plant species typical of alpine grasslands (*Carex bigelowii*, *Empetrum hermaphroditum*, *Hieracium alpinum*, *Juncus trifidus*) did not occur in dwarf pine plantations,

**Table 2.** Diversity parameters (mean ± s.e.) of the three compared habitat types at the two localities (Tabulové kameny, Keprník). Two analyses are presented, one for all species and the other for endangered species only. The size of relevé groups was standardised to 20 relevés. The Sørensen dissimilarity index was used to calculate beta-diversity. Post hoc comparisons on cell means of alpha diversity of all species were conducted using Fisher's LSD test at  $P = 0.05$ , while 95% confidence intervals of parameter estimates were used for alpha diversity of endangered species and beta diversity. Cell means significantly differing from each other are marked by different letters in a superscript.

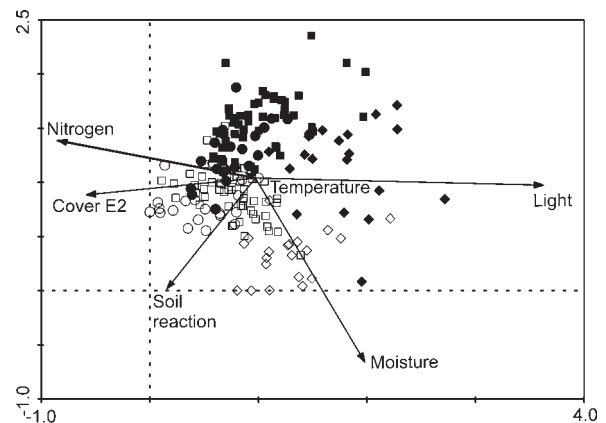
Diversity parameters / habitats	All species				Endangered species			
	Keprník		Tabulové kameny		Keprník		Tabulové kameny	
	mean±	s.e.(95%CI)	mean±	s.e.(95%CI)	mean±	s.e.	mean±	s.e.
<b>Alpha diversity</b>								
Dwarf pine	5.7 <sup>a</sup> ±	0.3	10.0 <sup>c</sup> ±	0.5	0.3 <sup>a</sup> ±	0.1	0.1 <sup>a</sup> ±	0.1
Gaps	7.0 <sup>b</sup> ±	0.3	8.7 <sup>b</sup> ±	0.3	0.9 <sup>b</sup> ±	0.2	0.5 <sup>b</sup> ±	0.2
Alpine grasslands	9.5 <sup>cd</sup> ±	0.5	9.6 <sup>cd</sup> ±	0.5	1.5 <sup>b</sup> ±	0.2	1.5 <sup>b</sup> ±	0.3
<b>Beta diversity</b>								
Dwarf pine	0.418	(0.413-0.422)	0.284	(0.282-0.287)	-	-	-	-
Gaps	0.433	(0.429-0.435)	0.363	(0.360-0.365)	-	-	-	-
Alpine grasslands	0.449	(0.444-0.455)	0.349	(0.344-0.353)	-	-	-	-
<b>Gamma diversity</b>								
Dwarf pine	19		21		2		2	
Gaps	19		22		3		3	
Alpine grasslands	24		24		6		5	

**Table 3.** Relative frequencies (%) of plant species in the three habitats at the two studied localities. Frames mark species typical of a particular habitat based on the analysed data. Species in bold are considered endangered according to the Red list of vascular plants of the Czech Republic (Procházka 2001).

	Alpine grasslands		Gaps		Dwarf pine stands	
	Tabulové kameny	Keprník	Tabulové kameny	Keprník	Tabulové kameny	Keprník
<b>Diagnostic species</b>						
<i>Eriophorum vaginatum</i>	30	30				
<i>Hieracium alpinum</i>	10	30				
<i>Empetrum hermaphroditum</i>	10	5				
<i>Juncus trifidus</i>		30				
<i>Deschampsia cespitosa</i>	20	15	24			
<i>Cetraria islandica</i>		50		6		
<i>Dicranum scoparium</i>	25	25			5	10
<i>Festuca supina</i>	100	20	67	8	10	
<i>Calluna vulgaris</i>	20	65		16		5
<i>Carex bigelowii</i>	5	60		16		5
<i>Bistorta major</i>	90	75	96	40	85	25
<i>Polytrichum formosum</i>	80	45	25	18	85	10
<i>Solidago virgaurea</i> subsp. <i>minuta</i>	80	10	33	8	25	15
<i>Nardus stricta</i>	10	15	4	8		
<i>Cladonia</i> sp.	5	20		40	5	
<i>Ligusticum mutellina</i>	20		27	12		5
<i>Luzula luzulooides</i> subsp. <i>rubella</i>	15	50	69	66	30	55
<i>Pleurozium schreberi</i>			10	44		
<i>Calamagrostis villosa</i>	60	80	67	86	100	90
<i>Trientalis europaea</i>	30	50	63	38	80	75
<i>Dryopteris dilatata</i>			4	2	55	35
<i>Rubus idaeus</i>			14		30	
<i>Veratrum album</i> subsp. <i>lobelianum</i>			2		20	
<i>Silene vulgaris</i>			4			20
<b>Common and accidental species</b>						
<i>Avenella flexuosa</i>	100	100	94	98	100	100
<i>Vaccinium myrtillus</i>	75	70	80	78	95	50
<i>Homogyne alpina</i>	65	55	80	24	75	25
<i>Vaccinium vitis-idaea</i>	50	30	53	60	80	25
<i>Rumex arifolius</i>	10		31		35	5
<i>Anthoxanthum alpinum</i>		10	6	22	5	
<i>Polytrichum commune</i>	40		12		45	
<i>Oxalis acetosella</i>			4	2	15	
<i>Sphagnum</i> sp.	5				15	
<i>Potentilla</i> sp.				4		5
<i>Huperzia selago</i>		5				
<i>Picea abies</i>				4		
<i>Hieracium</i> sp.				2		
<i>Polygonatum verticillatum</i>						10

whereas no endangered species were found just in dwarf pine stands (Table 3).

DCA analysis (Fig. 2) revealed a general pattern in the variation of species composition in the studied habitats over localities. The first ordination axis explained 9.3% of the total variation in species data and was associated with the gradient from the alpine grasslands on the right side of the ordi-

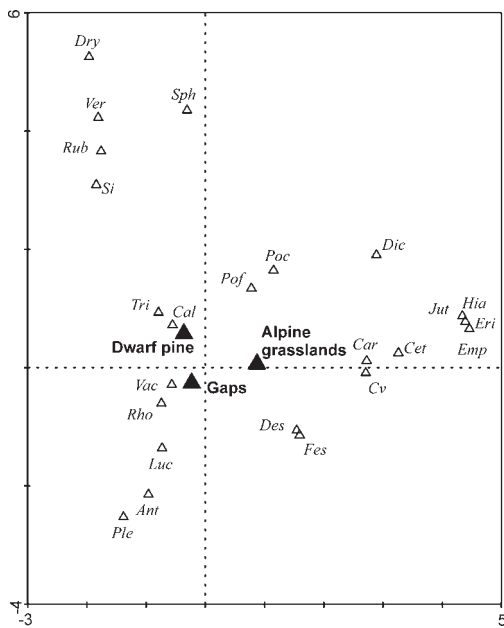


**Figure 2.** Joint plot (DCA) of samples from alpine grasslands (diamonds), gaps (squares) and dwarf pine stands (circles) at the two localities (Keprník – black symbols; Tabulové kameny – open symbols), and passively projected vectors of Ellenberg indicator values (light, soil reaction, moisture, temperature, nitrogen) and shrub layer cover (E<sub>2</sub>).

nation diagram through gaps within dwarf pine stands to the closed dwarf pine stands on the left. The second ordination axis explained 6.7% of the variability and corresponded mainly to the effect of locality. Therefore, the impact of dwarf pine on species composition overrode differences in species composition between localities. The species composition of gaps was intermediate between alpine grasslands and dwarf pine stands but was also more heterogeneous than in those habitats. The fact that ordination results (Fig. 2) were in compliance with beta-diversity values (Table 2) suggested that: (1) under dwarf pine stands, the heterogeneity of species composition was low at both localities; and (2) samples from Keprník were generally more heterogeneous than those from Tabulové kameny.

To eliminate the effect of locality, we partialled out this variable using partial CCA. As a result, we obtained the net





**Figure 3.** Joint pCCA diagram of species and environmental variables (habitats) with localities used as blocks. Herb layer: Ant – *Anthoxanthum alpinum*, Cal – *Calamagrostis villosa*, Car – *Carex bigelowii*, Cv – *Calluna vulgaris*, Dry – *Dryopteris dilatata*, Emp – *Empetrum hermaphroditum*, Fes – *Festuca supina*, Hia – *Hieracium alpinum* agg., Jut – *Juncus trifidus*, Luc – *Luzula luzuloides* subsp. *rubella*, Mut – *Ligusticum mutellina*, Pol – *Polygonatum verticillatum*, Rho – *Vaccinium vitis-idaea*, Rub – *Rubus idaeus*, Si – *Silene vulgaris*, Tri – *Tridentalis europaea*, Vac – *Vaccinium myrtillus*, Ver – *Veratrum album* subsp. *lobelianum*. Moss and lichen layers: Cla – *Cladonia* sp., Dic – *Dicranum scoparium*, Ple – *Pleurozium schreberi*, Poc – *Polytrichum commune*, Pof – *Polytrichum formosum*, Sph – *Sphagnum* sp.

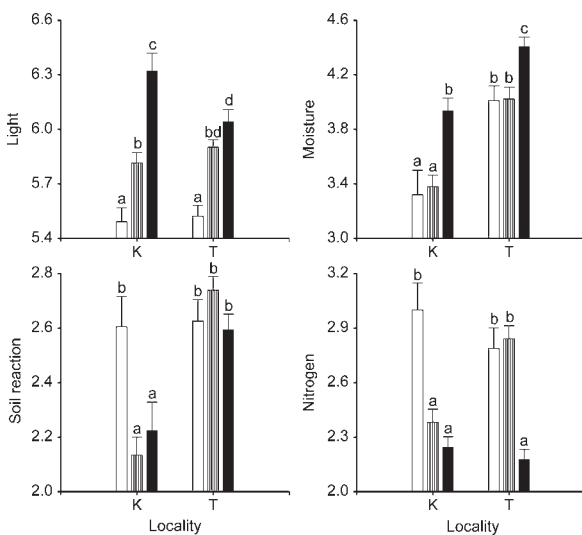
**Table 4.** General linear models testing the effects of locality and habitat on Ellenberg indicator values for light, temperature, moisture, soil reaction and nitrogen. Locality and habitat were considered as fixed factors (DF<sub>E</sub> = 175).

Source term	Light		Temperature		Moisture		Soil reaction		Nitrogen	
	DF	P	P	P	P	P	P	P	P	
Locality	1	0.174	0.067	<0.001	<0.001	0.449				
Habitat	2	<0.001	0.400	<0.001	0.075	<0.001				
Locality × habitat	2	0.031	0.955	0.731	<0.001	<0.001				

effect associated with the three habitat types. Significant differences in species composition were found among the habitats (pCCA, Monte Carlo permutation test of the first axis, eigenvalue = 0.178, *P* = 0.002; all axes, trace = 0.276, *P* = 0.002). Habitats explained 9.2% of the total variation in species composition after fitting covariables. Also, pair-wise comparisons between habitats revealed significant differences in species composition in all cases (pCCA, all *P* ≤ 0.002). It is evident from Fig. 3 and Table 3 that many characteristic alpine grassland species either not occurred (*Eriophorum vaginatum*, *Hieracium alpinum* agg., *Juncus trifidus*, *Empetrum hermaphroditum*, *Deschampsia cespitosa*) or their frequency was lower (*Dicranum scoparium*, *Cetraria islandica*, *Festuca supina*, *Calluna vulgaris*, *Carex bigelowii*) in other habitats. On the other hand, some species only occurred or had a higher frequency in dwarf pine stands (*Dryopteris dilatata*, *Rubus idaeus*, *Silene vulgaris*, *Veratrum album*, *Calamagrostis villosa*, *Tridentalis europaea*). Some species common in alpine grasslands also successfully survived in gaps and dwarf pine stands (*Avenella flexuosa*, *Homogyne alpina*, *Vaccinium myrtillus*, *V. vitis-idaea*).

*Ellenberg indicator values*

As expected, the mean Ellenberg values for light were lowered in the direction alpine grasslands > gaps > dwarf pine stands at both localities (Figs 2, 4; Table 4). On the other hand, no effects of locality or habitat on the Ellenberg indicators for temperature were observed. Localities strongly differed in Ellenberg indicators for moisture with Tabulové kameny being more humid than Keprník. However, similar trends between habitats were observed at both localities, where moisture indicator values were significantly lower in dwarf pine stands and gaps than in alpine grasslands. The Ellenberg indicators for soil reaction did not differ between habitats at Tabulové kameny. At Keprník, dwarf pine stands showed a soil reaction indicator value comparable to Tabulové kameny but higher than in the other two habitats. At both localities, low and similar mean values for nitrogen were found in alpine grasslands. The nitrogen indicator values were higher in both dwarf pine stands and gaps at Tabulové kameny, but at Keprník only in dwarf pine stands (Table 4, Fig. 4).



**Figure 4.** Mean (+ SE) Ellenberg indicator values for moisture, light, soil reaction and nitrogen in the studied habitats (white = dwarf pine plantation, hatching = gaps, black = alpine grasslands) at the two localities (K = Keprník, T = Tabulové kameny). Post hoc comparisons on cell means were made using Fisher’s LSD at *P* = 0.05.

**Discussion**

*Species diversity*

Changes in alpha diversity as a consequence of expanded dwarf pine stands has been documented in some Central-

European mountains where *Pinus mugo* is indigenous. The low values of alpha diversity for dwarf pine stands were in particular ascribed to light restriction under the canopy compared with open alpine grasslands (Svoboda 2001, Soukupová et al. 2001a, Wagnerová 2001a, b, Wild and Wildová 2002). Surprisingly, we observed a strong negative influence of dwarf pine stands on alpha diversity at Keprník but no clear pattern at Tabulové kameny. We consider the decline of alpha diversity in dwarf pine stands at Keprník to be the effect of two coinciding events: extinction of strictly heliophilous plant species typical of alpine grasslands (see Table 2 and Figs 2, 4) combined with the fact that this is locally not compensated for by an increase in frequency or immigration of species commonly occurring in dwarf pine stands. The absence of clear trends in alpha diversity at Tabulové kameny is probably related to the slightly lower age of dwarf pine plantings and the partly different composition of alpine grasslands (see Fig. 2), e.g., lower frequencies of competitively weaker mosses and lichens compared to those at Keprník (Table 3). Results from other mountains have documented temporal changes in the composition of understorey species accompanied by shifts in competitive interactions (Choler et al. 2001). Moreover, the age of plantings has been linked to habitat parameters such as soil type, humidity and vegetation type (Grashof-Bokdam and Geertsema 1998). In the Giant Mts. younger (i.e., more recently planted) dwarf pine stands showed higher alpha diversity than older (i.e., earlier planted) ones (Wild and Wildová 2002).

Our results showed that both the beta and gamma diversity of stands invaded by dwarf pine were lower than those of alpine grasslands. Montane woody vegetation has a relatively higher species pool than alpine grasslands on siliceous bedrock (Sádlo et al. 2007), but the process of saturation of relatively recently planted dwarf pine stands by species allochthonous to alpine grasslands is slow. Hence, this species saturation process is unable to compensate for the disappearance of alpine grassland species due to dwarf pine plantings, at least on the spatio-temporal scale examined.

### Species composition

Non-native dwarf pine was demonstrated to have a strong impact on the species composition of vegetation at both localities. Characteristic species of alpine grasslands typical of the Hercynian Mts. (Kočí 2007a) either not occurred or showed a low frequency under the influence of dwarf pine (Table 3). On the other hand, our results showed that the long-term persistence of dwarf pine stands can support species like *Trientalis europaea* and *Dryopteris dilatata* which are characteristic of montane spruce forests (Jirásek 1996b). Moreover, these species together with *Veratrum album* are common components of the natural communities formed by *Pinus mugo* scrub in other Hercynian mountain ranges (Jirásek 1996a). These species alone are not capable of colonising alpine grasslands.

Many plant species common in alpine grasslands, e.g., *Avenella flexuosa*, *Vaccinium myrtillus*, *Homogyne alpina*,

and *Vaccinium vitis-idaea*, also persisted under dwarf pine stands (Table 3). However, these species have a wider ecological amplitude and also occur in subalpine *Vaccinium* vegetation, subalpine tall grasslands (Kočí 2007a,b) and even in montane spruce forests (Jirásek 1996b) and dwarf pine communities (Jirásek 1996a). All these vegetation units border alpine grassland stands in the Hrubý Jeseník Mts. (Kočí 2007a, b). The response of these species to the presence of dwarf pine is therefore ambiguous.

The species composition of gaps suggests an intermediate position of such stands between alpine grasslands and dwarf pine stands, as well as an ecotonal effect of dwarf pine stands on adjacent alpine grasslands (Soukupová et al. 2001a,b).

### Ecological indicators

Bioindication showed increased shading for alpine grasslands → gaps → dwarf pine stands. Siemann and Rogers (2003) considered the modification of light conditions as one of the most important factors modifying the environment by shrubs during their expansion to grasslands. Both in the Giant Mts. (Málková et al. 2001, Wagnerová 2001b) and at our localities, the spread of dwarf pine was linked with a decreased frequency or complete extinction of heliophilous species. Decline of heliophilous species and spread of shade-tolerant plants in alpine stands invaded by shrubs have also been documented in other Central-European mountains (Blažková and Březina 2003, Pavlů et al. 2005, Špinlerová and Martinková 2006, Janišová et al. 2007).

Concerning moisture conditions, dwarf pine stands caused shifts in Ellenberg indicator values towards drier conditions. Striking differences in moisture between dwarf pine stands and alpine grasslands were also found in the Giant Mts. (Soukupová et al. 2001a, Wild and Wildová 2002). Consequently, the environment under the dwarf pine canopy is relatively dry, which is reflected in the understorey plant species composition.

While no conspicuous differences in the soil pH indicator among habitats were found at Tabulové kameny, even higher indicator values for soil pH were found in dwarf pine stands compared with both gaps and alpine grasslands at Keprník. We explain this pattern as a result of the nursing effect of dwarf pine, which allows the persistence of species with their optimum on moderately to weakly acidic soils and simultaneously with higher demands for soil nutrients, e.g., *Silene vulgaris* and *Veratrum album* subsp. *lobelianum* (Ellenberg et al. 1992). This is in line with higher indicator values for nitrogen in dwarf pine versus alpine grassland stands at both localities. Dwarf pines are able to intercept precipitation with dissolved pollutants (incl. NO<sub>x</sub>) more effectively than alpine herbs (Ellenberg et al. 1986, Eliáš et al. 1995, Soukupová 2001a, b). Although nitrogen deposition loads may vary per locality depending on wind direction and intensity, real deposition can reach nearly 50 kg N ha<sup>-1</sup> as NO<sub>x</sub> (Soukupová et al. 1995, Fabiszewski and Břej 2000). Nitrogen deposition

loads thus potentially raise the trophy level under dwarf pine stands faster than in alpine grasslands.

### Conservation implications

In terms of clonal growth and seed production, dwarf pine can accelerate its spread to alpine grasslands at a rate presently estimated as 2% of plantations area per year in the Hrubý Jeseník Mts. (Tremel et al. 2010b). While dwarf pine spreads only slowly via clonal propagation beyond the originally planted area at Tabulové kameny, intensive clonal propagation and high seed production was observed in dwarf pine at Kerpník (Šenfeldr 2008). Shading and a strong mass effect thus contribute to the spread of dwarf pine, and under such conditions dwarf pine can be considered an invasive species, in analogy to the situation in some parts of the northern Alps (Dullinger et al. 2003).

We consider the colonisation of alpine grasslands by dwarf pine unacceptable from a conservation point of view in the Hrubý Jeseník Mts. Dwarf pine plantation here (i) influences not only microclimatic conditions and unique morphological processes in soils (Tremel and Křížek 2006), but (ii) its spread potentially threatens adjacent sites of high biodiversity which harbour high numbers of endangered species including relicts and endemic species (Jeník et al. 1980, 1983a,b, 1998). Moreover, (iii) the localities studied are part of nature reserves and Sites of Community Interest (Natura 2000) of the highest conservation priority in the Czech Republic (Kavalcová and Kavalec 2003). We showed that many endangered alpine grassland plant species go extinct, and shifts in community structure take place during the dwarf pine colonisation process. Alpine communities generally cover only a small area of medium-high mountains. This is also true for the Hrubý Jeseník Mts., where subalpine and alpine communities presently cover about 11 km<sup>2</sup> in comparison to 2 km<sup>2</sup> of dwarf pine stands (Tremel and Banaš 2008). Hence, the spread of dwarf pine is a stronger threat to biota in mountains with smaller alpine areas than those with an extensive alpine zone. It is highly important to understand the ecology of communities profoundly before reducing dwarf pine when making management and monitoring programmes.

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