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Long-Term Changes in Dwarf Pine (*Pinus mugo* Turra) Cover and Growth in the Orava Beskid Mountains, Slovakia

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Dwarf pine (Pinus mugo *Turra*) *thickets are a substantial land cover in high-elevation mountain ecosystems in Europe, where they fulfill important functions in soil conservation and as wildlife habitat. In many areas across Europe these thickets have rapidly expanded over the past decades because of changing climate and land use, highlighting the need to better understand how species spread relates to growth traits and changing environmental conditions. We quantified changes in dwarf pine cover by elevation on 2 mountains in the Western Carpathians (Central Europe) over 64 years (Babia hora) and 40 years (Pilsko), and we linked them to species growth responses to climate using archival photogrammetry and stem length measurements. We correlated mean growth chronologies with mean monthly temperature and precipitation to assess the main climatic factors driving growth. The total expansion of dwarf pine cover was substantial (28.6% in Babia hora and 57.1% in Pilsko), but the rate of expansion varied with elevation, site, and intra- and interspecific competition. The largest expansion occurred in the open stands of the high elevations (1550–1650 m). Statistically significant positive correlations between growth and temperature were recorded for the most recent growing season and for the preceding growing season. However, despite rising temperatures over time, mean species growth during the last 20 years decreased slightly. The correlation of growth with precipitation was mostly positive but not statistically significant. Thus, the impact of changing climate appeared too weak to overcome other influential factors (eg decline in grazing and intra- and interspecific competition).*

Keywords: *Species spread; alpine treeline; climate change; growth sensitivity; archival photogrammetry; length increment.*

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Introduction

High-elevation plant communities in European mountains are often dominated by dwarf pine (*Pinus mugo* Turra) (Tsaryk et al 2006), which fulfills important functions in preventing soil erosion, increasing water retention, and providing wildlife habitat. In the Western Carpathians, a subalpine belt dominated by homogeneous thickets of dwarf pine well adapted to extreme conditions occurs between 1500 and 1800 m independently of the substrate (Lukáčik 1999). In the past, the distribution of dwarf pine in the Western Carpathians was negatively affected by grazing by sheep and cattle, with dwarf pine communities reduced to approximately 20% of their original extent in areas that were unsuitable for grazing and replaced by alpine meadows elsewhere (Tsaryk et al 2006; Jodłowski 2007).

After World War II, socioeconomic changes in Central Europe left their imprint on the relationship between the environment and society (Burkovský 2006). With the onset of socialism, extensive protected areas with good infrastructure for nature protection were developed (Knorn et al 2012; Mihai et al 2017). After grazing had ceased in protected areas, dwarf pine cover increased to about 40% of its original extent (Tsaryk et al 2006), often because of extensive reforestation (eg Jodłowski 2007) carried out to reduce the risk of erosion and avalanche formation and to increase evapotranspiration (Sokol 1965).

The understanding of growth processes in dwarf pine thickets is important for predicting temporal dynamics

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and spatial distribution of this vital alpine ecosystem (Wild and Winkler 2008; Palombo et al 2010). Unlike most pine species (eg, Dovčiak et al 2005), spatial spread of dwarf pine depends not only on seed dispersal and germination, seedling survival and growth, competition with other plants, and disturbance regime, but also on its ability to reproduce vegetatively (Wild and Winkler 2008) by forming polycormones (multistemmed clones), which spread horizontally (Vorčák and Jankovič 2009; Treml et al 2010). This occurs most frequently in plant communities formed by *Vaccinium myrtillus* L., together with *Vaccinium vitis-idaea* L., *Deschampsia cespitosa* L., *Avenella flexuosa* L., *Nardus stricta* L., and *Juncus trifidus*, which are usually dominant in subalpine localities in the Western Carpathians (Vorčák and Jankovič 2009; Treml et al 2010). However, the growth and competitive ability of dwarf pine changes significantly with increasing elevation because of changing environmental conditions and declining competition from other woody species (Takahashi and Yoshida 2009).

In addition to cessation of grazing, global climate warming has been suggested as an important factor driving the spread of dwarf pine (Dirnböck et al 2003; Harsch 2009; Treml et al 2010). While Melo (2005) showed an increase in average temperature in Slovakia over the past 50 years maximally by 1.4°C, in the longer time period 1881–2017 there was an increase of 1.73°C with an average decrease in total precipitation of 0.5% (Ministry of Environment 2017). Dwarf pine distribution can be reduced by the expansion of trees colonizing the lower parts of the dwarf pine vegetation belt, but it can expand to higher elevations as climate warming may offset adverse climatic conditions and lengthen the growing season there (Wada et al 2005; Takahashi and Yoshida 2009). Consequently, relic alpine meadows above the dwarf pine belt may be threatened by climate warming and dwarf pine expansion on mountains of lower elevation. Because of their competitive ability, compact cover, and vegetative regeneration, expanding dwarf pine thickets can exert a strong negative influence on the biodiversity of alpine meadows by reducing habitat for heliophytic alpine plants and many insect species (Kuras et al 2001). The dynamics of polycormone spread may, therefore, be one of the most important issues in biodiversity conservation in mountain areas with the occurrence of dwarf pine affected by the changing climate (see Treml et al 2010).

In alpine ecosystems, species growth and distribution are particularly sensitive to changing climatic conditions (Körner 1994; Grabherr et al 2000). A changing growth rate is generally considered to be a valuable indicator of tree response to changing environmental conditions (Bär et al 2006; Wason et al 2017). Trees and shrubs growing above the treeline tend to have a prostrate growth form (Dai et al 2017) with radial growth characterized by frequent occurrence of compressed wood and missing or wedging annual tree rings (Schweingruber 1996; Bär et al 2006). This makes it difficult to measure radial tree growth by tree rings. In dwarf pine, this difficulty can be overcome by focusing instead on annual stem length increments, which are more substantial, regular, and easily detectable due to scars on the bark (Takahashi and Yoshida 2009), as commonly measured in numerous studies (eg Kajimoto 1993; Wada et al 2005; Kyncl 2006; Špinlerová and Martinková 2006; Maděra et al 2011; Lukáčik et al 2014). Combining this approach with photogrammetry using historical and recent aerial images can be a powerful tool for detecting patterns and drivers of changes in the distribution of dwarf pine thickets in mountain landscapes affected by changing climate (eg Mihai et al 2007; Treml et al 2010; Švajda et al 2011; Solár 2013; Solár and Janiga 2013; Dai et al 2017).

In this study, we investigated the spatial dynamics of dwarf pine on 2 mountains in the Orava Beskids section of the Western Carpathians over several decades (from 1949 to 2013). Our main objectives were to quantify and contrast changes in dwarf pine cover in areas of both natural recolonization and reforestation, and to examine if dwarf pine growth and thus distribution may be changing because of changing climate.

Material and methods

Study area

The study was conducted at 2 sites, on the mountains Babia hora and Pilsko, located in the Slovakian portion of the Orava Beskids, a mountain range in the Western Carpathians (*Supplemental material*, Figure S1, http://dx.doi.org/10.1659/MRD-JOURNAL-D-18-00049.S1). Babia hora, with a summit elevation of 1725 m, is the highest peak in the Orava Beskids. Pilsko is a separate massif with a summit elevation of 1557 m. The bedrock of the Orava Beskids is Magura-flysch, and the most frequently represented soil types are podzolic Cambisols, Rankers, and Podzols, while humic Podzols dominate in higher elevations (Lukniš et al 1972). Average annual temperature is 2°C (6°C in the growing season), average annual precipitation is 1600 mm (600–700 mm in the growing season), and snow cover lasts on average from October to May (Lukniš et al 1972). The study sites were located above the alpine treeline, where forest composition changes gradually from forests dominated by Norway spruce (*Picea abies* (L.) H. Karst.) to dwarf pine and juniper (*Juniperus communis* var. saxatilis Pall.) stands. The plant communities of the area belong to the phytosociological class *Loiseleurio-Vaccinieta* Eggler ex Schubert 1960, order *Rhododendro-Vaccinietalia* Br.-Bl. et Jenny 1926, and alliance *Vaccinion myrtilli* Krajina 1933 (Kliment et al 2007).

Based on historical forest management plans, in Pilsko, the natural spread of dwarf pine was augmented substantially by reforestation carried out in the mid-1970s

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TABLE 1 Main characteristics of aerial imagery used to map dwarf pine distribution.[a)]

	Year			
	1949	1973	1992	2013
Flight altitude (m)	–	5700	5000	4050
Camera type	RB 20/30	WILD	LMK15	UltraCamXp
Calibrated focal length (mm)	200. 14	114.72	152.27	100.5
Format	230 × 230 mm	180 × 180 mm	230 × 230 mm	17,310 × 11,310 pixels
Image overlap (%)	30	>60	>60	>60
Resolution, scanned/ground/ortho (μm/m/m)	–/–/0.5	15/0.63/0.5	15/0.41/0.5	6/0.25/0.5
Number of aerial images used	Existing orthophotomap provided by Geodis Slovakia, s.r.o. (http://mapy.tuzvo.sk/HOFM/)	17	22	163

[a)] Sources: 1949: *Historical Orthophotomap of Slovakia* (2013); 1973 and 1992: *Historical black and white aerial images* (Topographic Institute, Banská Bystrica, Slovakia); 2013: *True-color digital images* (National Forestry Centre, Zvolen, Slovakia). Not all data were available for 1949.

using a chessboard planting pattern to increase the stability of snow and soil layers; the total planted area was approximately 17 ha in the elevation zone 1450–1550 m and 1.5 ha in the elevation zone <1450 m . (Unfortunately, planting details and maps were not preserved to clearly and consistently separate these plantings from the surrounding natural populations.) Reforestation with dwarf pine did not occur on Babia hora. The study areas are designated National Nature Reserves with the highest degree of protection; no intervention is permitted except for the maintenance of hiking trails.

Data collection and analysis

We used digital photogrammetry to analyze spatial distribution and temporal changes in dwarf pine cover, and field measurement of annual stem (length) growth increments to measure dwarf pine growth.

Spatial distribution and temporal changes: To reconstruct dwarf pine cover, we selected and analyzed historical and recent aerial images. A dataset for 1949 was extracted from the Historical Orthophoto Map of Slovakia (2013). Additional datasets were extracted from black-and-white aerial images taken in 1973 and 1992 (Topographic Institute, Banská Bystrica, Slovakia, 2016) and from true-color digital images taken in 2013 (National Forestry Centre, Zvolen, Slovakia, 2013) (Table 1). The 1949 aerial data for Pilsko were incomplete and were excluded from analysis.

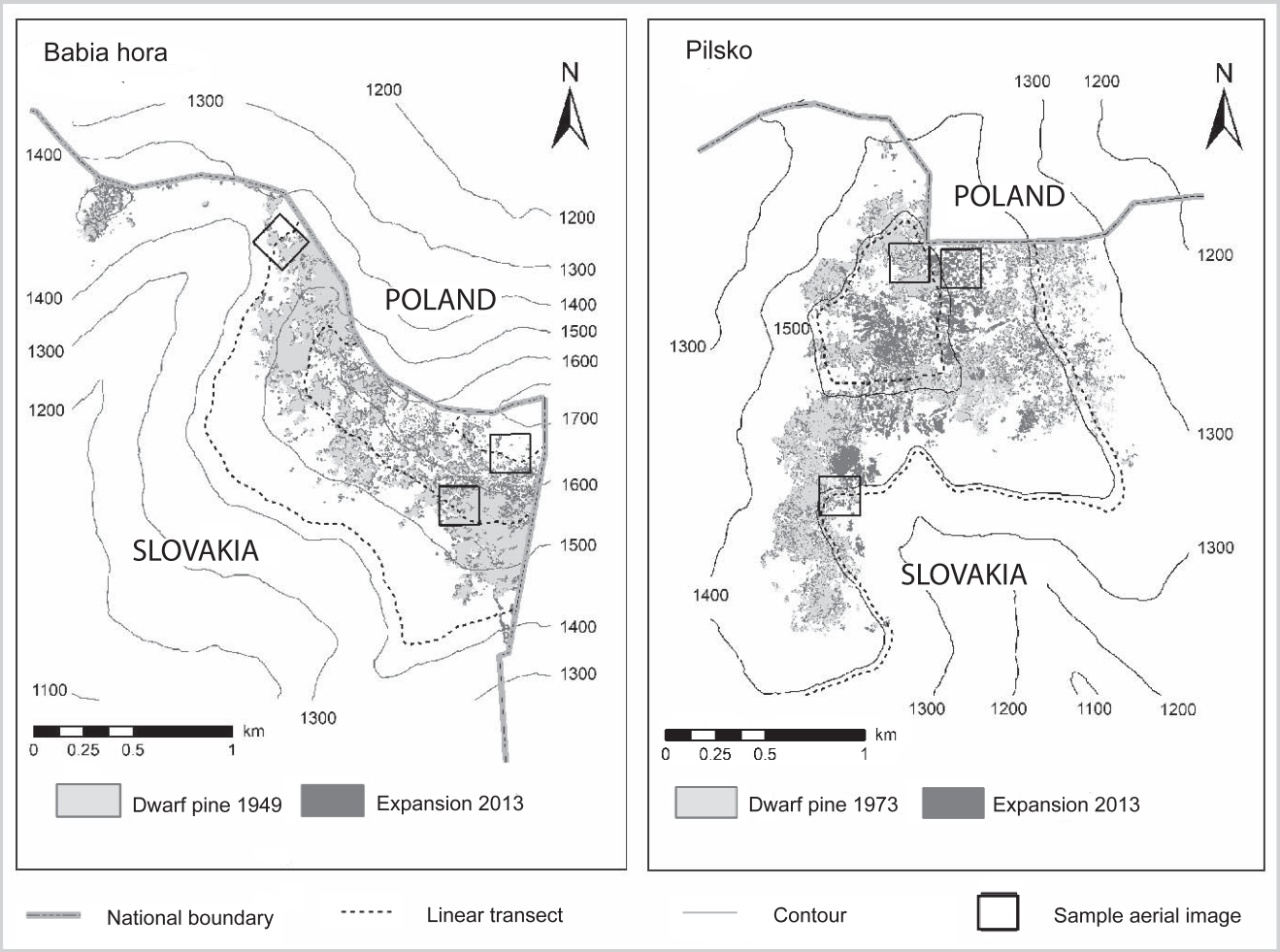
Data processing consisted of 3 levels: digital photogrammetry, image classification, and geographic information systems (GIS) analysis with cartographic representation.

A combination of traditional methods of aerotriangulation and orthorectification (eg Wolf and Dewitt 2000; Mikhail et al 2001) and some specific workflows for archival photogrammetry (eg Prokešová et al 2010) were used to obtain spatially correct orthoimages. The workflow started with interior orientation of the images. Then the exterior orientation for individual images was computed using automatic aerotriangulation with iterative bundle block adjustment, in which least-squares adjustments were applied to the ground control points (Prokešová et al 2010) in order to obtain the best solution for the triangulation equations. Historical aerial images with computed exterior orientation parameters were orthorectified using the same digital elevation model (5 m grid) generated from the 2013 images with 0.5 m resolution orthoimages.

Object-oriented classification was performed according to the methodology presented in Treml et al (2010), based on the multiresolution segmentation of raster layers and following classification of segments using a combination of nearest neighbor classifier and membership functions resulting in 2 classes: dwarf pine and others. Despite this methodology, a number of manual classifications had to be done to obtain reliable and comparable measures of the area of dwarf pine cover in a given period. The accuracy of automatic object-oriented classification was computed based on the training test area mask (*Supplemental material*, Figure S2, http://dx.doi.org/10.1659/MRD-JOURNAL-D-18-00049.S1), which served as a correct reference layer containing manually corrected dwarf pine cover for each period. The results of these classifications were analyzed using Cohen's Kappa statistic (Cohen 1960), where values for the kappa index of agreement range from 0 to 1. According to

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FIGURE 1 Dwarf pine expansion on Babia hora (1949–2013) and Pilsko (1973–2013), as delineated from aerial photographs, with the location of the linear transects used in the study and the aerial photographs shown in Figures 2 and 3. (Maps by authors)



Landis and Koch (1977), values greater than 0.80 represent strong agreement, and values between 0.40 and 0.80 represent moderate agreement.

Data representing the dwarf pine cover area were analyzed in GIS by study site and elevation zone: <1450 m, 1450–1550 m, and >1550 m. Pilsko's highest elevation is 1557 m, and thus it does not have a >1550 m zone.

Dwarf pine's natural spread over time was evaluated directly from the aerial imagery by analyzing changes in the dimensions (object-oriented classification) of its polycormones over time (1973–2013) as a function of study site, elevation zone, competition from spruce (present versus absent), and direction of spread (following contour lines versus slope). Polycormones were selected for analysis from the aerial images (≥20 polycormones for each elevation zone and competition variant on each site) only when they had clearly identifiable borders that allowed unambiguous delineation of separate polycormones on old and new images. Significant differences in polycormone spread over time were tested using one-way ANOVA with a post-hoc Tukey HSD (Honest Significant Difference) test.

Field measurements: To corroborate the biological basis for the dwarf pine spread quantified from the aerial imagery, we carried out field measurements of annual dwarf pine stem (length) growth increments in June 2017 using visible growth scars on the bark. (Since growth was not completed for 2017 in June, this length increment was not analyzed.) Annual length increments were measured along linear transects following contour lines (1 per elevation zone, totaling 3 transects on Babia hora and 2 on Pilsko; see Figure 1) on 40 stems that intersected the transects (with an accuracy of 1 mm from the stem tip to root collar, excluding 2017 growth). The statistical sample size was determined following Bartlett et al (2001). Mean length increment chronologies were developed for each elevation zone and study site. Polynomial functions were fitted to length increments to assess their trends over time. Goodness of fit was verified through linear regression.

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TABLE 2 Development of dwarf pine cover by elevation zone and time period on Babia hora and Pilsko. Babia hora is taller than Pilsko and has aerial photography available from 1949, while the first aerial photographs of Pilsko are from 1973.

Zone	Initial area	1949–1973		1973–1992		1992–2013		Total change		
	ha	ha	% yr^{-1}	ha	% yr^{-1}	ha	% yr^{-1}	ha	%	% yr^{-1}
Babia hora										
1400	2.80	–0.64	–1.0	0.47	1.1	0.83	1.5	0.66	23.6	0.4
1500	44.35	0.73	0.1	4.08	0.5	3.66	0.4	8.47	19.1	0.3
1600	5.49	1.79	1.4	1.50	1.1	2.62	1.4	5.91	107.7	1.7
Pilsko										
1400	22.75	–	–	5.87	1.4	2.88	0.5	8.75	38.5	1.0
1500	34.71	–	–	12.68	1.9	11.54	1.2	24.22	69.8	1.7

The homogeneity of length increments was evaluated by the pointer year method, which shows annual growth reactions due to abrupt changes in environmental conditions (especially in climate; Schweingruber 1996). Pointer years (Py) are characterized by reduced (Py ≤ -1) or increased (Py ≥ 1) increments relative to immediately preceding or following years (5-year mowing window). We further analyzed tree growth sensitivity by estimating the annual expression (morphological expression of an event year, Schweingruber 1996) as the percentage of individual stems that were above or below the Py thresholds (≤ -1 or ≥ 1) in any particular year.

To identify climatic factors controlling dwarf pine growth, correlations between mean length increment chronology and mean monthly weather characteristics (temperature and precipitation) were computed using long-term data for the Orava Beskids obtained from the CRU (Climate Research Unit) TS3.21 dataset (0.5×0.5° grid interpolated points) (Harris et al 2014). The correlations were performed using a 17-month window (from April of the previous year to August of the analyzed year) to include climate variation during the period most influential on tree growth (Dirnböck et al 2003; Treml et al 2010).

Results

Spatial distribution and temporal changes in dwarf pine cover

Dwarf pine thickets were restricted to mountain summits, where they covered 67.7 ha (Babia hora) and 90.3 ha (Pilsko) in 2013 (Figure 1). The overall dwarf pine cover increased by 28.6% on Babia hora over 64 years and by 57.1% on Pilsko over 40 years. The expansion rate varied with time, elevation, and site (*Supplemental material*, Figure S2, http://dx.doi.org/10.1659/MRD-JOURNAL-D-18-00049.S1). On Babia hora, the total expansion rate was quite low at lower and middle elevations (zones <1450 m and 1450–1550), and it was considerably higher at high elevations (>1550 m zone), where the total cover more than doubled between 1949 and 2013 (Table 2). On Pilsko, the largest annual expansion occurred in 1973–1992, following (and partly because of) largely successful reforestation with dwarf pine during this period (about 17 ha planted in the 1450–1550 m zone and 1.5 ha in the <1450 m zone). Dwarf pine continued to spread rapidly in 1992–2013, at higher annual rates in middle elevations and lower rates at lower elevations (Table 2).

These patterns of dwarf pine spread over time are well illustrated by aerial photographs. On Babia hora, dwarf pine thickets tended to be compact (continuous) at middle and low elevations, where they co-occurred with spruce and little open alpine grassland was available for colonization, while at high elevations, dwarf pine occurred mainly in small patches scattered within the matrix of alpine meadows (Figure 2). In contrast, dwarf pine thickets on Pilsko were often patchy and surrounded by alpine grassland even at middle and lower elevations in 1973, providing ample space for dwarf pine expansion by 2013 (Figure 3).

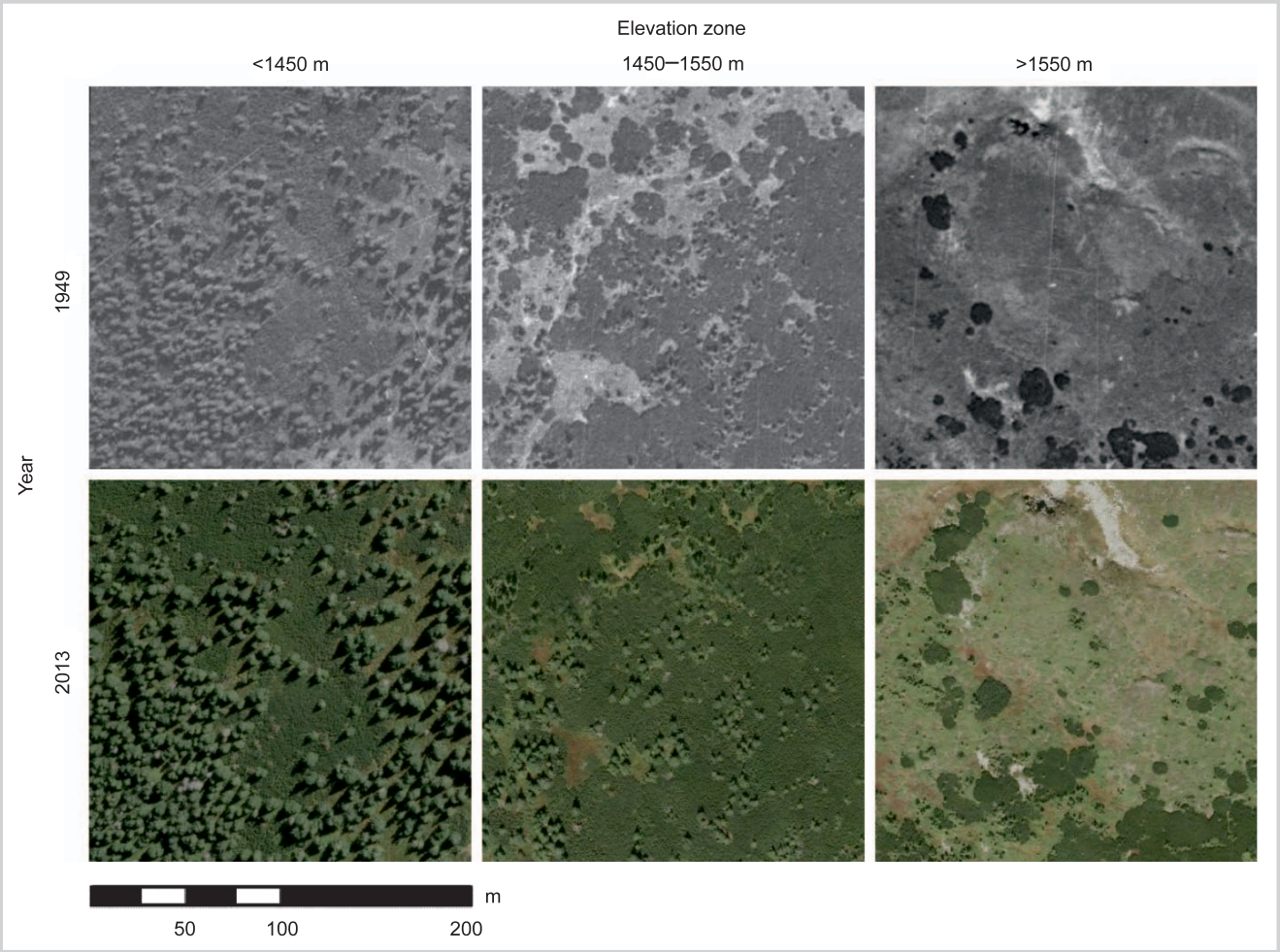
At middle and lower elevations, the spatial spread of individual dwarf pine polycormones was significantly affected (decreased) by competition from spruce but not by site or elevation (Table 3). These statistically significant differences in polycormone spread over time with and without spruce competition were confirmed for both elevation zones and both directions of polycormone growth on Pilsko. (On Babia hora, the number of polycormones fulfilling selection criteria was too low for analysis.)

Patterns and controls of dwarf pine growth

Mean annual length increments varied between sites and elevation zones. In general, annual length increments were greater in middle elevations than in high or lower elevations, and they were lower in Pilsko than in Babia hora (Table 3). The mean length increment chronologies of the individual elevation zones further corroborated that growth was generally greater at middle elevations than at high or lower elevations, and that growth at

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FIGURE 2 Aerial photographs showing the natural distribution of dwarf pine thickets on Babia hora in 1949 and 2013 by elevation zone. Each photograph represents an area of 4 ha (200 × 200 m). Dwarf pine thickets show as smooth dark grey or dark green patterns; lighter shades of gray or green show alpine grassland vegetation, while larger crowns visible at <1450 and 1450–1550 m belong mainly to Norway spruce (*Picea abies*).



middle elevations appeared to first increase and then decline over time on Babia hora, while temporal trends in other elevations and on Pilsko were less pronounced (Figure 4, left). Despite these differences, the mean length increment chronologies of the individual elevation zones were significantly correlated with each other on both sites (all $P < 0.01$; Babia hora 0.45, 0.66; Pilsko 0.52), making it possible to average the chronologies of each site (Figure 4, right).

We identified several pointer years after 1973, characterized by abrupt changes in dwarf pine growth (Babia hora: 12, Pilsko: 14) (Figure 4, right). The majority (80%) of the pointer years were the same for the 2 sites, suggesting that dwarf pine growth varied over time in similar ways at both sites. However, the mean annual expression (mean percentage of stems responding to pointer years positively or negatively) was quite low on both sites (ranging from 13% to 16%), with a significant (exhibited on >50% of trees) annual growth response not occurring at all on Babia hora and occurring only twice on Pilsko (negative in 2014 and positive in 2016) (Figure 4, right).

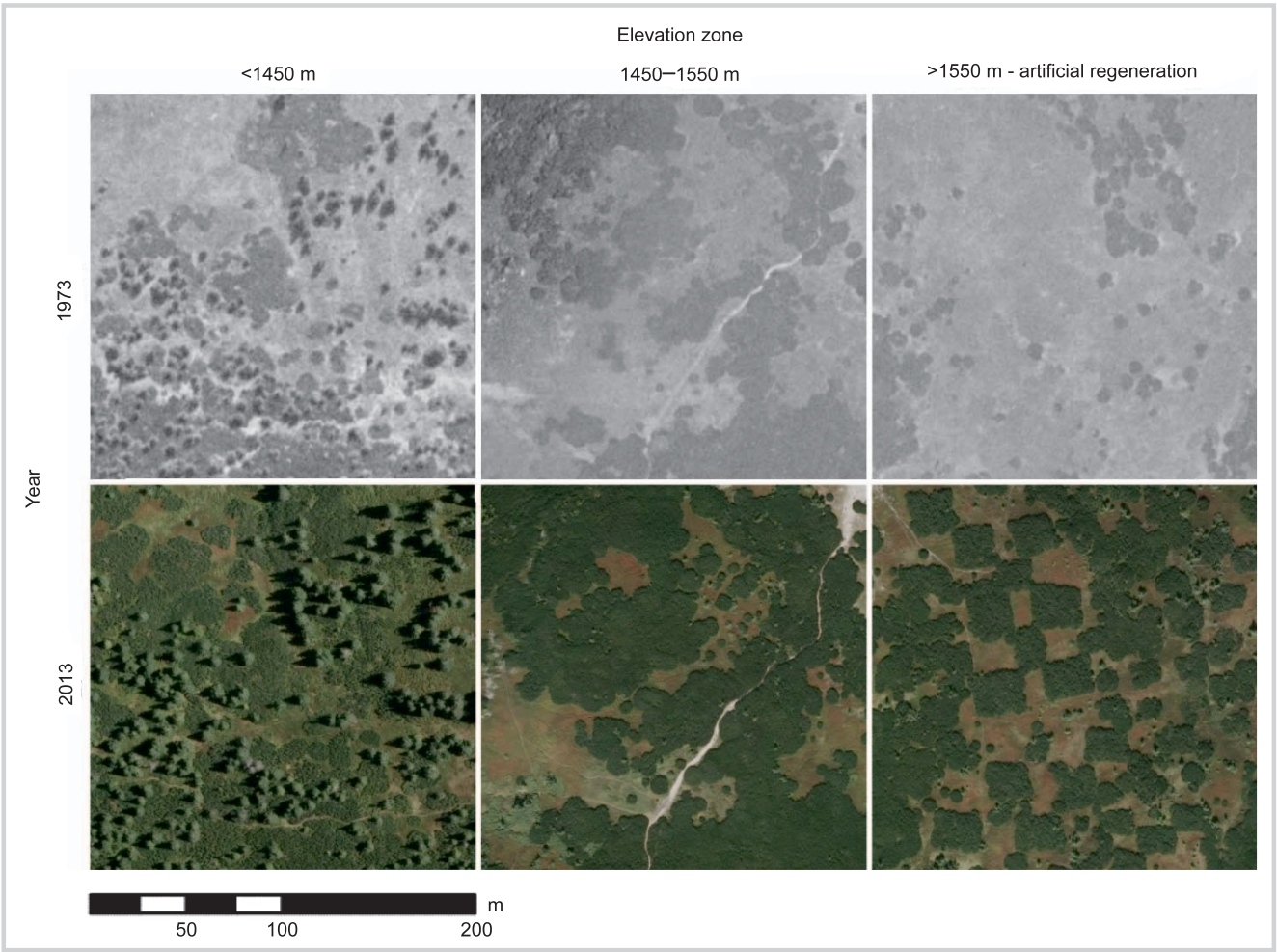
Due to the similarity of the 2 sites in climate and dwarf pine growth, they were pooled together to investigate the relationship of dwarf pine growth to climate. Statistically significant positive correlations of mean growth chronology and monthly temperature were recorded for the growing season when growth occurred and the preceding growing season (Figure 5). The correlations of mean growth chronology with monthly precipitation were not statistically significant.

Discussion and conclusions

Dwarf pine spread over time in our study varied with elevation as it integrated declining growth and changing inter- and intraspecific competition with elevation, as corroborated by other studies (Takahashi and Yoshida 2009; Vorčák and Jankovič 2009). Our study area (the Orava Beskids) is characterized by the coldest climate in

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FIGURE 3 Aerial photographs showing the distribution of dwarf pine thickets on Pilsko in 1973 and 2013 by elevation zone. Each photograph represents an area of 4 ha (200 × 200 m). The 4 photographs on the left show naturally established thickets, while the 2 photographs on the right show dwarf pine plantings (artificial regeneration), visible as dark green squares on the 2013 photograph. See Figure 2 caption for additional interpretation of the photographs.



the Western Carpathians, with the upper forest limit almost 100 m lower (at 1350–1450 m above sea level) than on other mountains in the region (Vorčák and Jankovič 2009). This is consistent with the relatively low cover of dwarf pine and the presence of spruce in the <1450 m zone in our study. Spruce can occur at higher elevations on southwestern aspects (as it did in our study), where it vigorously competes with dwarf pine, while dwarf pine can descend to lower elevations in areas where spruce is excluded because of poor substrate or an unfavorable local microclimate (eg talus slopes or terrain depressions with snow accumulation) (Tranquillini 1979; Mihai et al 2007; Carcaillet et al 2009; Treml et al 2010). Despite strong competitive pressure from spruce in the lower elevations, dwarf pine was still able to spread into open areas and substantially increase over time (naturally by 23.6% on Babia hora, and by 38.5% on Pilsko, where natural populations were augmented by plantings).

Although the largest natural dwarf pine cover on Babia hora was in the middle elevations, dwarf pine expansion in this zone was relatively modest (19.1%), reflecting that much of the area was already colonized by this species (see Pagan and Randuška 1987; Wild and Winkler 2008). The largest increase in dwarf pine cover (>100% over 64 years) occurred at the high elevations, where dwarf pine formed patches scattered within the grassland matrix; studies on other mountains also suggested fast spread rates for scattered dwarf pine polycormones (60% increase over 40 years, Treml et al 2010; the greatest expansion rates in high elevations, Mihai et al 2007). Thus, our study adds evidence that dwarf pine can rapidly expand into alpine meadows as documented elsewhere in Slovakia (eg Švajda et al 2011; Solár 2013; Solár and Janiga 2013) and across Europe (eg Mihai et al 2007; Carcaillet et al 2009; Palombo et al 2010; Dai et al 2017). This dwarf pine expansion is consistent with woody invasions of montane meadows following their abandonment, for example cessation of hay making or grazing (Dovčiak et al 2015), and with upward vegetation shifts induced by climate warming (Harsch et al 2009). As the climate has

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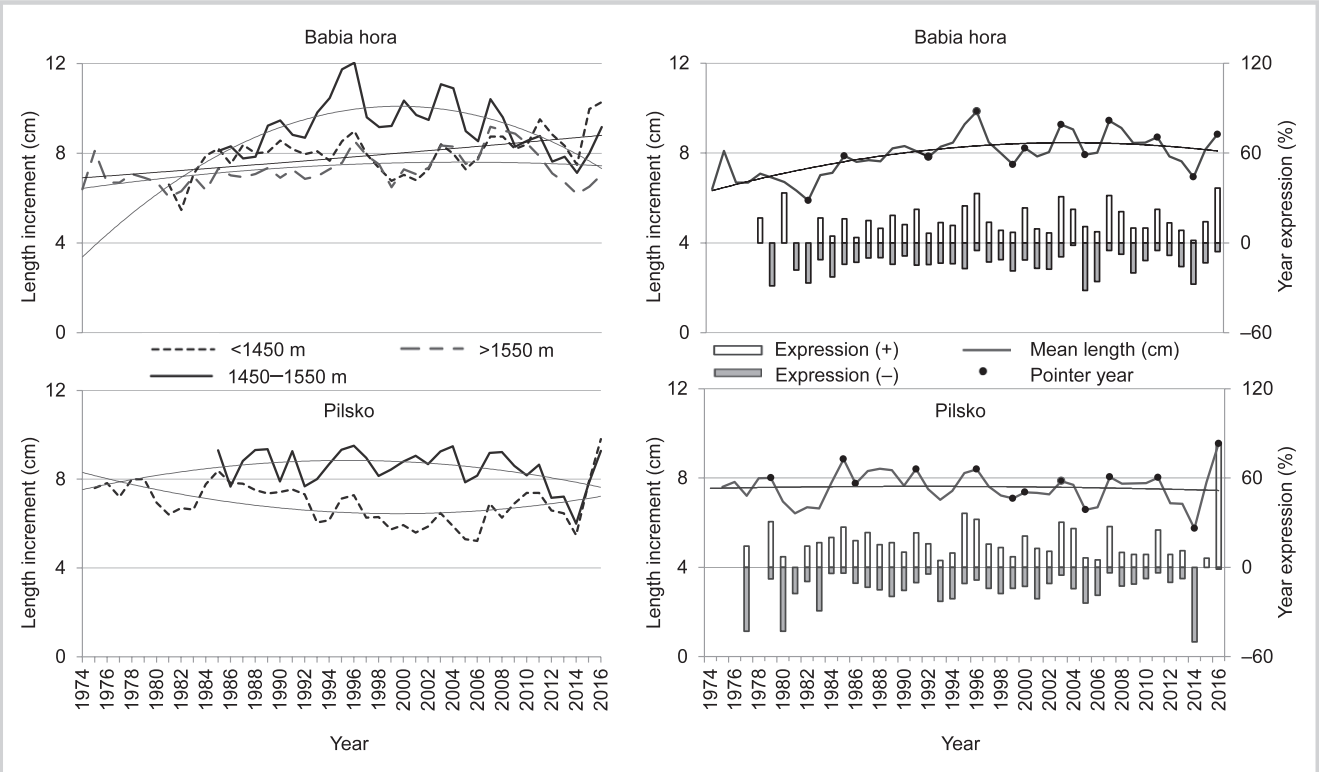
TABLE 3 Dwarf pine growth over time: length increment of stems and spread of polycormone by study site, elevation zone, and presence of spruce competition (mean ± SD). Letters indicate statistically significant ($P \leq 0.05$) differences.

Zone	Competition	Polycormone spread (m/40 yr)		Length increment (cm yr^{-1})
		Along contour line	Perpendicular to contour line	
Babia hora				
1400	No	3.5 ± 6.7[a]	4.4 ± 5.4[a]	8.15 ± 2.29[c]
1500	No	7.4 ± 5.6[a]	6.9 ± 3.3[a]	9.32 ± 2.86[a]
1600	No	2.3 ± 5.5[a]	3.7 ± 4.2[a]	7.43 ± 2.20[d]
Pilsko				
1400	No	4.8 ± 3.7[a]	4.9 ± 2.8[a]	6.78 ± 2.25[e]
	Yes	–1.9 ± 2.5[b]	–2.1 ± 3.8[b]	
1500	No	4.9 ± 2.6[a]	5.2 ± 2.8[a]	8.47 ± 2.67[b]
	Yes	–0.7 ± 4.2[b]	–1.4 ± 5.1[b]	

become warmer (by 0.7 to 1.4°C) and drier at high elevations in Slovakia over the past 50 years (Melo 2005), our study lends some support to the climate change hypothesis (dwarf pine growth was positively related to temperature) but more to the land-use change hypothesis (dwarf pine growth did not continue to increase consistently over time with warming).

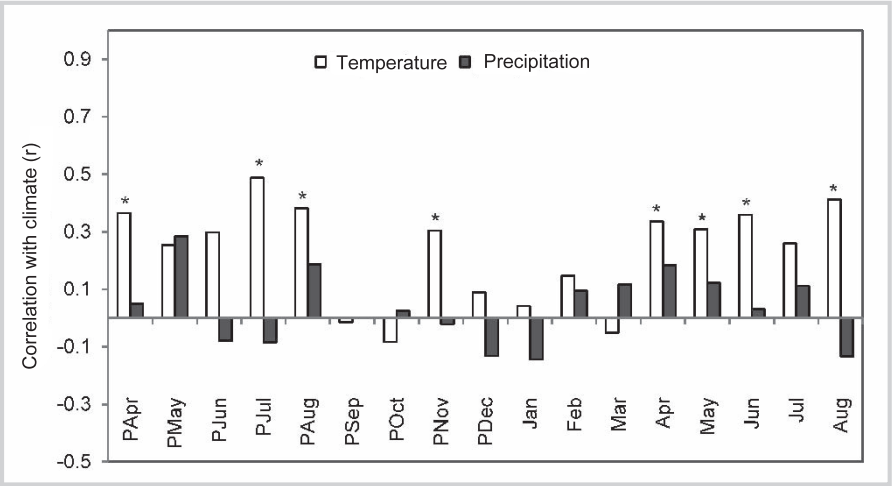
In contrast to the natural spread on Babia hora, dwarf pine spread on Pilsko was augmented by chessboard plantings that substantially increased its cover during

FIGURE 4 Mean length increment chronologies per elevation zone (left) and their site means with annual expressions and pointer years (Py) (right) for Babia hora and Pilsko. Polynomial fits are shown only as an aid in interpreting the graphs (goodness of fit expressed by $R^2 = 0.2–0.5$). Py were not evaluated when sample size dropped below 5 individuals. Annual expression was measured as the percentage of stems with positive or negative growth responses in any particular year.



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FIGURE 5 Correlations between mean growth chronology and mean monthly temperature and precipitation for 1974–2013. Correlations were calculated using a 17-month window from April of the previous growing season to August of the year when the growth occurred. Months of the previous growing season are marked with P. Asterisks indicate statistically significant correlations ($P < 0.05$).



1973–1992 and facilitated continuing species expansion in the post-planting 1992–2013 period. Thus, reforestation by dwarf pine appears to be a viable management strategy for avalanche and soil erosion control in mountain areas where forest cover has been reduced by grazing or other disturbance (see García-Hernández et al 2017). The high rate of expansion in the middle elevations on Pilsko (nearly 70% over 40 years) contrasted with much slower expansion from the natural populations on Babia hora in this elevation zone (about 19% over 64 years), suggesting that the chessboard planting pattern allowed rapid expansion from planted patches into the open spaces among them, similar to the expansion occurring from the scattered dwarf pine patches at the high elevations on Babia hora (>100% over 64 years). Both the checkerboard plantings on Pilsko and the naturally patchy distributions of dwarf pine on Babia hora provide support for the efficacy of cluster plantings in the reforestation of high mountain ecosystems (Schönenberger 2001).

Dwarf pine spread over time can be strongly affected by nearby vegetation (Dirnböck et al 2003); it can be particularly successful in communities dominated by the low shrubs (eg *Vaccinium myrtillus* and *Vaccinium vitis-idaea*) and grasses (eg *Avenella flexuosa* and *Festuca airoides*) (Treml and Šenfelder 2007) that formed communities in our study (phytosociological class *Loiseleurio-Vaccinieta*; Kliment et al 2007). These communities occur often in higher elevations, and they may potentially facilitate upward spread of dwarf pine as the climate continues to warm. On the other hand, in lower and middle elevations, spruce appeared to negatively affect the spread of dwarf pine polycormones, likely because of competition for light (Jeník and Lokvenc 1962; Treml et al 2010). As warmer climate is expected to shift the treeline and spruce distribution upward, the negative effects of spruce on dwarf pine are likely to intensify and cause the eventual decline of dwarf pine at the margins of its lower elevational range.

Dwarf pine growth varied somewhat between the 2 mountains in our study. This was likely because of edaphic, microclimatic, or vegetation factors (see Takahashi and Yoshida 2009; Lukáčik et al 2014), since the 2 mountains had a similar regional climate. The mean annual length increments in our study (Babia hora: 7.43–9.32 cm/yr; Pilsko: 6.78–8.47 cm/yr) were similar to growth reported elsewhere in Central Europe (6.4–8.6 cm, Maděra et al 2011; about 8 cm, Kyncl 2006). However, growth clearly varied across elevations; it was the largest in middle elevations and decreased in high elevations (where climate became more adverse; see Takahashi and Yoshida 2009) and in lower elevations (where competition from spruce increased). The 1450–1550 m zone appeared to be an optimum elevation for dwarf pine growth in the long term, but the growth in natural populations on Babia hora decreased in this zone over the last 2 decades (after reaching the highest values in the 1980s and mid-1990s), probably as a consequence of increasing intraspecific competition. At high and lower elevations where dwarf pine cover was lower, growth trends were less clear, but they appeared to exhibit a weak upward trend consistent with positive climate warming effects on growth (see *Pinus pumila* growth in Japan; Wada et al 2005).

The lower growth sensitivity to climate was confirmed in our study by annual expressions (only 13–16% of individuals responded to climate on average), while the 2 years with significant growth responses (both on Pilsko) were not related to temperature or precipitation. Growth may reflect other climatic or environmental factors (eg snow cover duration, Dirnböck et al 2003; insect pests, Lukáčik et al 2014). Yet growth in our study did respond positively to temperature, as suggested by the correlations of our length increment chronology with monthly climate variables (particularly with temperature means for April–

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August and the previous growing season), corroborating similar findings by Dai et al (2017). Temperature and precipitation were closely related to various dwarf pine life stages: the onset of photosynthesis and wood formation in April–May and maximum cell production in June–July (Büntgen et al 2007), and the maturation of needles, shoots, and buds in late summer and autumn (Dirnböck et al 2003; Treml et al 2010; Dai et al 2017). While our study provides moderate evidence that changing climate may have partially driven dwarf pine expansion in the Orava Beskids, other factors (particularly decline in grazing) may have been more important in facilitating the rapid spread of dwarf pine across all elevation belts.

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Supplemental material

FIGURE S1 Location of study sites (Babia hora: 49.573050, 19.529548; Pilsko: 49.528001, 19.316791). (Map by authors)

FIGURE S2 Dwarf pine cover evaluated from aerial imagery in individual years and confusion matrixes based on training test area masks. (Maps by authors)

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