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Ecotonal dynamics of the altitudinal forest limit are affected by terrain and vegetation structure variables: an example from the Sudetes Mountains in Central Europe

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Abstract

At the landscape scale, the response of alpine treelines to increasing temperatures often varies due to second-order factors such as terrain properties, vegetation structure, and land use. In this study, we examined the influence of topographic and vegetation-structure variables on spatial patterns of treeline ecotone shifts in the Sudetes Mountains (Czech Republic). The changing positions of the alpine timberline and alpine treeline were determined from orthogonal aerial images allowing comparisons between 1936 and 2005. Our results showed that the alpine timberline advanced upward at an overall rate between 0.30 m yr^{-1} in the Hrubý Jeseník Mountains (eastern part of the Sudetes) and 0.43 m yr^{-1} in the Giant Mountains (western part of the Sudetes). Forest infilling was substantially greater than advances above original alpine treeline positions. Forest upward shifts occurred mostly on sites with already established, well-dispersed trees and low levels of prostrate dwarf pine cover. Topographic variables such as altitude and heat load affected forest advance if initial tree cover was low. The occurrence of competitive prostrate shrubs and the presence of climatically extreme convex parts of slopes appear to be important second-order factors affecting treeline ecotone shifts, particularly at wind-affected treelines.

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Introduction

Mountain ecosystems worldwide have recently undergone accelerated changes in response to rising temperatures (Walther et al., 2002), and many European mountain landscapes have also been altered by agricultural land abandonment (Tasser et al., 2007; Rössler et al., 2008; Améztegui et al., 2010). Both factors lead to the advance of upper forest limits, which may have serious consequences for alpine biodiversity (Theurillat and Guisan, 2001). In this study, we focus on the alpine treeline ecotone, which is a transitional zone between the upper limit of closed forest (i.e., alpine timberline) and the upper limit of the occurrence of tree species (Körner, 2012). Whereas the position of the alpine timberline results from the interaction of several factors including climatic variables and disturbances, the location of the tree species limit is governed by temperatures (Holtmeier, 2009; Körner, 2012). An intermediate position within the treeline ecotone is represented by the alpine treeline, which is conventionally delineated as a line connecting all the uppermost locations of tree stands (see exact definitions in the Methods section).

The main factors affecting the expansion and retreat of tree stands at their upper limits are scale-dependent (Holtmeier, 2009). At the global scale, treeline position is determined by growing-season temperatures (Körner and Paulsen, 2004), whereas at the landscape scale, second-order factors, in addition to temperature, significantly affect treeline altitude and dynamics (Holtmeier and Broll, 2005). These factors include climatic stress caused by wind or precipitation, natural disturbances (e.g., avalanches, debris-flows, insect outbreaks) and geomorphological factors (Holtmeier, 2009, and other references therein). Furthermore, recent or past human intervention, including cattle and reindeer grazing, can depress either entire treeline ecotones or their lower boundaries (Miehe and Miehe, 2000; Dalen and Hofgaard, 2005). Therefore, at the landscape scale, it is expected that, in addition to variability in temperature trends, the rate and extent of treeline advance or retreat are likely to be shaped by spatial variations in second-order factors. In particular, the patterns of near-ground temperatures, snow distribution, wind abrasion, and mass movement are expected to be reflected in the patterns of treeline advance or retreat (Dalen and Hofgaard, 2005; Holtmeier and Broll, 2005; Van Bogaert et al., 2011; Sutinen et al., 2012). In addition, differences in the invasibility of alpine plant communities can significantly affect forest expansion (Dullinger et al., 2003; Rössler et al., 2008; Wang et al., 2012).

Although recent upward advances of treeline ecotones are widespread in mountain regions (Harsch et al., 2009), our knowledge of spatial patterns in treeline ecotone shifts at the landscape scale is still surprisingly poor, except for some studies from subarctic areas and the Alps (Lloyd et al., 2003; Kullman and Öberg, 2009; Diaz-Varela et al., 2010; Stueve et al., 2011). We aim to fill this gap by assessing treeline ecotone shifts in the Sudetes Mountains, a mountain chain in Central Europe. In particular, our goal is to disentangle the effects of topographic and vegetation-structure variables on treeline ecotone shifts in an area subjected to temperature increase of 1 °C over the past 100 years (Głowicki, 1998) and to agricultural land abandonment. Indeed, both increasing temperature and agricultural land abandonment promote tree stand expansion (Motta et al., 2006), because they affect primary limiting mechanisms of tree occurrence in high elevations, that is, dieback, seedling mortality, and growth limitation (Harsch and Bader, 2011). In our study, treeline ecotone shifts were assessed over the past 70 years based on comparisons of a series of aerial images.

Methods

STUDY AREA

The Sudetes Mountains, a Hercynian mountain range on the border between the Czech Republic and Poland, reach their greatest heights in the Giant Mountains (highest peak: Mount Sněžka,

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1602 m) in the west and in the Hrubý Jeseník Mountains (highest peak: Mount Praděd, 1491 m) in the east (Fig. 1). The alpine area in the Giant Mountains (GM) is about 5500 ha, and about 1600 ha in the Hrubý Jeseník Mountains (HJ). The Sudetes are characterized by high elevation plateaus with adjacent steep slopes. Their treeline ecotones are usually situated in the upper or central parts of slopes at altitudes ranging from 1200 to 1400 m. In both mountain ranges, the position of about 20% of the length of the treeline is affected by extensive block fields and avalanche tracks (Treml and Banaš, 2000).

Climate is characterized by high precipitation (approximately 1400–1600 mm per year), an irregularly distributed snow pack, and a mean annual temperature of about 1 to 2 °C at the uppermost locations (Tolasz et al., 2007). The treeline trees experience strong western winds (Jeník, 1961) having mean wind speeds of more than 10 m s^{-1} (Tolasz et al., 2007). Low growing season temperatures (temperature of May–August is 6.7 °C at Sněžka climatic station, 1602 m) together with paleoecological data demonstrate the presence of a climatic treeline (Jeník and Štursa, 2003; Treml et al., 2008). The forests of the upper montane belt and treeline ecotone are composed of Norway spruce (*Picea abies* [L.] Karst.). Alpine and subalpine communities are dominated by graminoids, prostrate dwarf pine stands (*Pinus mugo*), and *Vaccinium* shrubs.

The extent of the alpine forest-free area was enlarged by deforestation and grazing from the early medieval period (9th–11th century A.D., Speranza et al., 2000; Novák et al., 2010) until the beginning of the 19th century, when mountain agriculture (grazing and grass mowing) peaked (Lokvenc, 1995). Direct human impacts then gradually diminished until the 1940s. Almost no direct human intervention in the treeline ecotone has occurred since then, as these areas became strictly protected as nature reserves. However, high-elevation forests in the Sudetes experienced acid air pollution, which resulted in marked growth depression of trees in the 1970s and 1980s (Kroupová, 2002).

DELINEATION OF THE ALPINE TREELINE ECOTONE

The position of the alpine treeline ecotone was characterized by two lines roughly corresponding to traditionally used terms, *alpine timberline* (hereinafter *timberline*—connecting all upper margins of closed forest) and *alpine treeline* (hereinafter *treeline*—connecting the highest outposts of forest on adjacent slopes partitioned by aspect).

Forests and forest-free areas were determined from true color or panchromatic aerial images provided by the Military Office for Geography and Hydrometeorology. Image resolution ranged from 0.25 to 0.32 m per pixel. Images were first orthorectified using OrthoEngine 9.0 (PCI Geomatica) with a digital terrain model (DTM) of 10-m resolution. Ground control points were collected from current orthogonal images (Czech Geodetic Survey). Root mean square error of orthorectification was not higher than 1.5 m for any image. Subsequent image segmentation and classification resulted in a binary matrix of "tree" and "no-tree" pixels (Definiens Professional 2006) (Fig. 2, parts A and B).

Image segmentation and classification were restricted to a manually delineated mask approximately covering the area upward

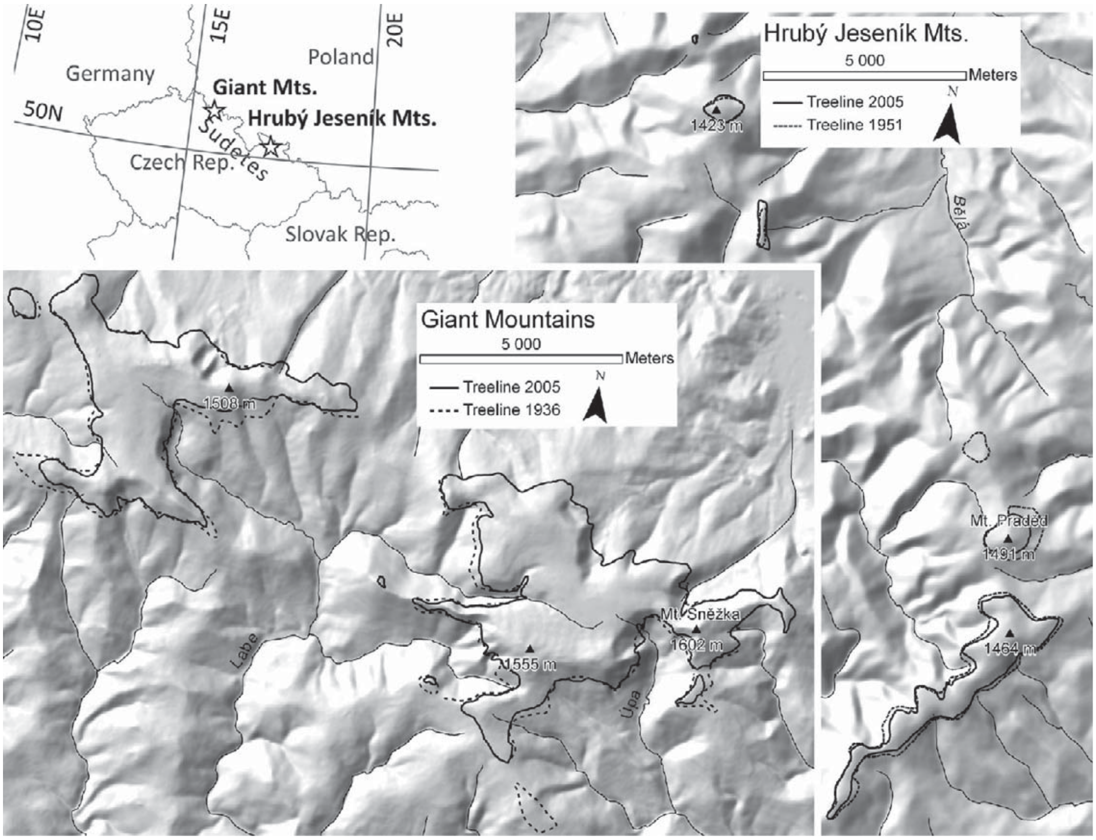

FIGURE 1. Location of the study area.

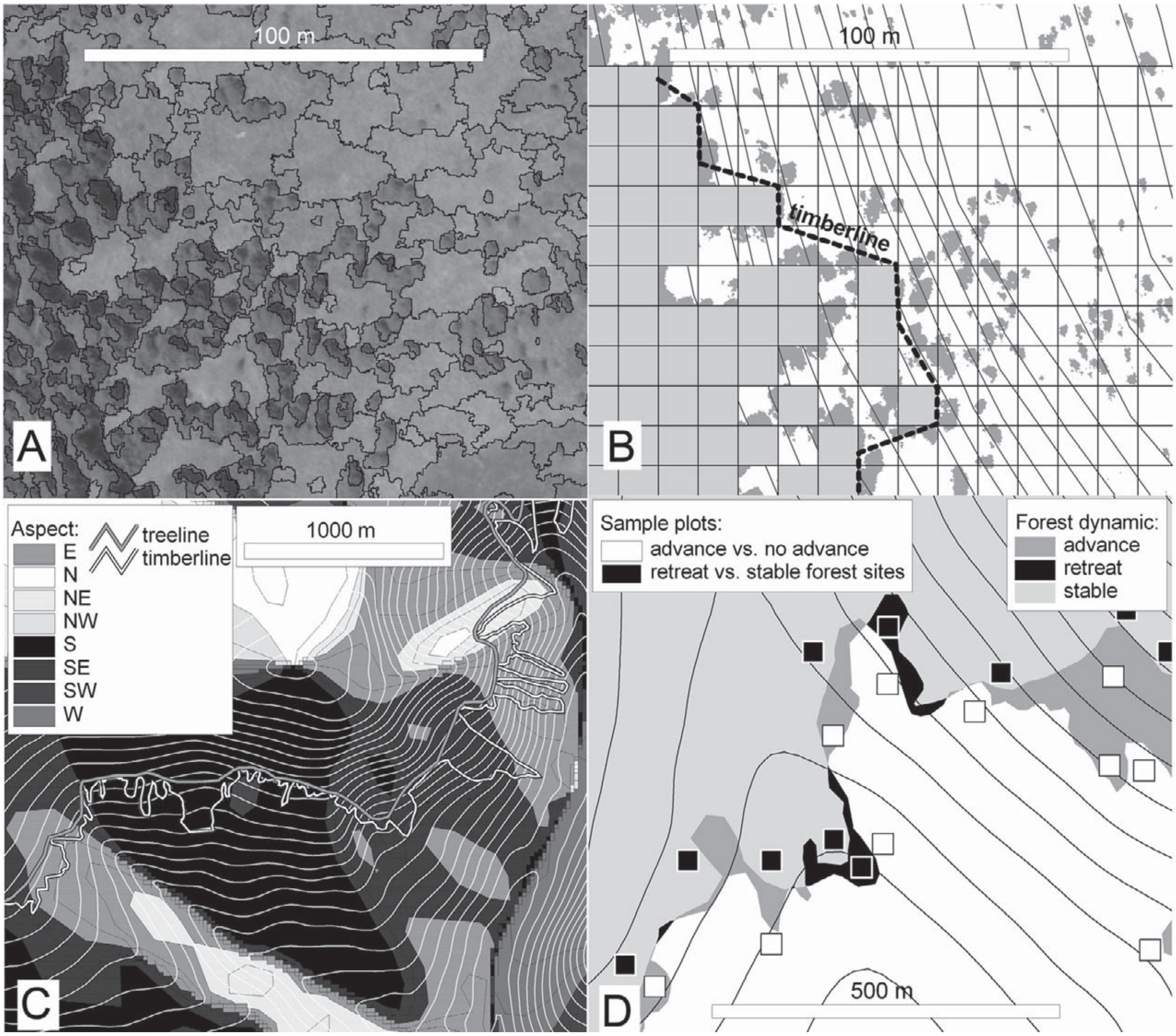

FIGURE 2. Delineation of alpine treeline and alpine timberline; (A) segmented image; (B) delineation of timberline on classified image; (C) delineation of treeline; (D) location of 30 m sample plots for analysis of spatial patterns of treeline ecotone shifts.

from the uppermost zone of closed forest (lower boundary located about 200 m below timberline). Segmentation was conducted hierarchically at two to three spatial scales. At the coarse level (scale = 100, shape = 0.3, compactness = 0.5), the spruces, dwarf pines, and spruce shadows were distinguished from grasslands, screes, and paths. At a finer level (scale = 20, shape = 0.3, compactness = 0.6), individual trees, shadows, and dwarf pines were delineated. For some images, an additional level with scale of 6, shape of 0.4, and compactness of 0.5 was applied. Trees were classified based on brightness parameter (distinguishing them from shadows) and on their neighborhood with shadows (distinguishing them from dwarf pines). To improve classification accuracy for differentiation between spruce and dwarf pine, we used layers of contemporary and past distributions of dwarf pine with pixel sizes of 0.5 m for 2005 image classifications, and, if available, also for historical aerial images (these layers were derived by on-screen vectorization; Hošek, 2007; Krkonoše Mountains National Park authority). Extensive manual corrections were necessary when classifying old panchromatic images, mainly due to low spectral resolution and the presence of scratches. Final classification accuracy of the spruce class (Producer's and User's accuracy; Congalton and Green, 1999) was about 81% for 1936 and 1953 images, 85% for images from the 1960s and 1970s, and 90% for orthogonal images from 2005 (Table 1).

For the purpose of our study, we defined timberline as a line connecting all of the neighboring highest positions of 10 × 10 m forested pixels (Fig. 2, part B) which were the result of superimposition of a 10 × 10 m regular mesh over the study areas. Highest neighboring forested pixels were searched within a radius of 100 m. The forested pixels were defined by a minimum tree cover of 50% (Jeník and Lokvenc, 1962), as the 50% threshold on a small area of 100 m^2 is a value traditionally used in the Czech Republic for the definition of forest (Jeník and Lokvenc, 1962). According to our observations, the same stands would in fact be characterized by ~30% canopy cover when examined at a larger scale.

The treeline was defined as a line connecting the highest positions of the timberline in adjacent slope sections which were divided into 45° wide aspect intervals (Fig. 2, part C). The treeline thus represents an idealized line that is relatively unaffected by local geomorphological factors and past anthropogenic disturbances.

TABLE 1

Producer's, User's, and Overall classification accuracy (Congalton and Green, 1999) of spruce class based on 500 randomly generated points belonging to the spruce class (Producer's accuracy) and 500 randomly selected visually identified spruces from sample plots (User's accuracy).

Image	Producer's accuracy (%)	User's accuracy (%)	Overall accuracy (%)
1936	77	85	81
1953	85	94	89
1964/1969	88	87	87
1973	84	95	89
2005	88	94	91

For both regions, we derived the positions of the timberline and treeline using images enabling comparison across the longest possible time span. They came from three different periods: (1) shortly after cessation of mountain agriculture (images from 1936 in GM and 1953 in HJ); (2) shortly before the cooling and acid pollution stress of the 1970s and 1980s (images from 1964–1969 for GM and 1973 for HJ); and (3) during recent times (i.e., 2005 images for both regions). For the sake of simplicity, the images from 1964 to 1969 from GM are hereinafter all called "1964." All subsequent computations of tree cover changes between individual time windows were standardized to the annual level. The selection of the study period was influenced by data accessibility and data quality; therefore, the particular years used differed between GM and HJ.

All analyses were processed using PCI Geomatica (orthorectification), Definiens Professional (segmentation, classification), and ArcGIS software (analysis of aspect, curvature, slope, altitude, heat load, timberline, and treeline delineation).

ANALYSIS OF ALPINE TREELINE ECOTONE SHIFTS

At the beginning of the analysis, all of the areas where the treeline ecotone was obviously directly affected by human activities (logging, spruce plantations) or avalanches were excluded. Then, successive timberlines and treelines were superimposed and a change map was created. For each period, the mean and maximum altitude for the entire timberline and treeline and for four aspect intervals (N, E, S, W) were computed based on DTM with 10-m resolution. Images were not available for a limited part of the area in the GM for the year 1936; therefore, only overlapping parts of the ecotone that were common to all successive time periods were compared. Annual changes of the timberline and treeline were calculated assuming linear shifts. Additionally, the overall area of retreats and expansions for a given period was computed, again with respect to the slope aspect. The areas of timberline expansion were divided into areas of ingrowth (below the original treeline position) and areas of real timberline advance (above the original treeline position). The resulting measurements of the areas of timberline shifts for each slope aspect were corrected for tectonic bias given that slopes in all aspects have equal area. Correction coefficients were computed as a real percentage of timberline length on a given slope aspect divided by the ideal percentage length (i.e., by 25%). They ranged from 0.96 to 1.07.

ASSESSING SPATIAL PATTERNS

In addition to comparing overall treeline ecotone shifts, we focused on their spatial patterns. Our approach used the random positioning of 30-m-square sample plots both in areas with an identified expansion of the timberline and in a 50-m-wide buffer upslope of the timberline position (Fig. 2, part D). Given the buffer's immediate proximity to the timberline position, we assumed it to have represented area for potential upward expansion, with the differences between buffer and the sites of actual expansion likely revealing site characteristics necessary for upward expansion. Sample plots inside the buffer were positioned using random sampling stratified by aspect, with the numbers of sample plots for each given aspect proportionate to the total area of slopes of that aspect. The 30 m size of sample plots reflected DMT and image resolution as well as the need for relative homogeneity of environmental characteristics within the plot. A minimum distance of 30 m between adjacent sample plots was adopted. In contrast to direct comparisons of changes in tree cover percentage, we believe our binary (forest/no forest) analytical approach to be more robust, given the typically low classification accuracy of historical panchromatic images.

For each sample plot, we derived topographic and vegetation structure variables affecting energy balance, intensity of slope processes, wind exposure, snow pack height, and available space for colonization by trees (e.g., Resler, 2006; Stueve et al., 2011). The following topographic variables were derived from the 10 m DTM as the average value of pixels inside an individual sample plot: altitude, slope, curvature, heat load index (Sensu McCune and Keon, 2002), and westness. Westness was computed by the symmetric division of aspect, resulting in a minimum westness value (0) assigned to east-facing slopes and maximum (180) to west-facing slopes. The vegetation structure was described using the following variables: number of trees, tree cover, mean basal area of tree crown (computed as tree cover/number of trees), dwarf pine cover, grassland cover, rock/scree cover, and nearest neighbor index of tree clustering (with Donnelly correction of edge effect, sensu Wong and Lee, 2005). Vegetation structure variables were determined by means of on-screen vectorization of individual cover classes (trees, dwarf-pine stands, grassland, scree/rocks). The number of trees and the nearest-neighbor clustering index were derived from points representing tree tops, identified by on-screen vectorization. Based on data resolution, we were able to distinguish trees ca. 2 m high. On-screen vectorization was conducted at a 1:800 scale. Data were collected for 553 (GM 1936–1964), 440 (GM 1964–2005), 290 (HJ 1953–1973), and 264 (HJ 1973–2005) sample plots. In total 31,559 trees were digitized.

For the proper evaluation of variables affecting timberline retreat, a set of 30 m sample plots positioned closely below the parts of the timberline that had not retreated was created. These sample plots, therefore, represent stable parts of forest. Topographic variables (altitude, slope, aspect, terrain curvature, and heat load index) derived from these sample plots were compared with those from retreating parts of the timberline. All analyses were processed using ArcGIS software.

STATISTICAL ANALYSES

The evaluation of spatial patterns of ecotonal shifts was performed separately for each region (GM and HJ) and for the early and late parts of the study period. Because retreats were represented by relatively few sample plots, the main statistical operations were completed using a binary response variable—"expansion"

TABLE 2

Annual altitudinal expansion or retreat of timberline and treeline. Values represent altitudinal shifts in meters (m yr^{-1}) assuming linear shift. Rates of increase of maximum timberline position are in parentheses.

	Giant Mountains		Hrubý Jeseník Mountains	
	1936–1964	1964–2005	1951–1971	1971–2005
N	+0.17	+0.30	+0.35	+0.11
E	+0.42	+0.08	+1.51	–0.29
S	+0.73	+0.27	+0.95	–0.08
W	+0.48	+0.87	+1.44	–0.29
timberline	+0.50 (+2.10)	+0.39 (+0.83)	+1.17 (+0.05)	–0.14 (+0.09)
N	+0.95	+0.05	+0.93	–0.14
E	+1,79	-0.14	+1.44	–0.30
S	+0.82	+0.08	+1.03	–0.19
W	+0.14	+0.39	+0.99	–0.18
treeline	+0.50	+0.09	+1.22	–0.21

and “no-expansion” (i.e., a “buffer”). We then compared variables characterizing areas in which the forest had expanded with the variable values of buffers, allowing us to ask which variables increased the probability of expansion. We used logistic regression or linear regression models within the framework of hierarchical partitioning (Chevan and Sutherland, 1991). This method reduces collinearity by identifying the independent contribution of each explanatory variable to the response variable and separating it from the joint contribution that reflects the correlation among variables (Walsh and Mac Nally, 2004).

Because we hypothesized that treeline advance would be strongly influenced by the initial cover of spruce trees, we performed separate analyses (i) with all uncorrelated variables including spruce cover and (ii) with all variables other than spruce cover. The response variable in the second type of analysis was represented by the residuals of a logistic model of expansion/no-expansion explained by spruce initial cover. The same analysis with residuals as a response variable was also performed for the sample plots categorized by initial spruce cover up to 15%, 15%–25%, and above 25%, to examine whether the variables’ influencing treeline advance differed according to initial spruce cover.

Prior to performing regressions, the correlation matrix of explanatory variables was computed. If the detected correlation between variables was higher than 0.5, only one of the correlated variables entered into the subsequent analysis. The variable was selected with respect to regression model performance as indicated by model deviance or R^2. Due to this exclusion, no analysis was performed with more than nine explanatory variables, thus avoiding the rounding error associated with hierarchical partitioning using numerous variables (Olea et al., 2010). Variables were Z-transformed prior to analysis in order to prevent large differences among the absolute values of different individual variables. For variance partitioning we used the “hier.part” package (version 1.0 and updates) (Walsh and Mac Nally, 2004) in the R statistical software (R Development Core Team, 2006). The significance of individual variables in hierarchical partitioning was tested by the Monte Carlo permutation test with 100 iterations. The goodness-of-fit of the overall model using all of the explanatory variables that underwent hierarchical partitioning was evaluated using the deviance percentage function in the “BiodiversityR” package (Kindt and Coe, 2005) or using R^2 in linear regression.

The differences in variables between plots with stable and retreating tree stands were analyzed using logistic regression within the framework of hierarchical partitioning.

Although we adopted the criterion of a minimum distance between sample plots, we also checked model residuals for spatial autocorrelation using the local Moran’s I method (Wong and Lee, 2005). If residuals were spatially autocorrelated, regression within hierarchical partitioning was applied after spatial eigenvector mapping (Dormann et al., 2007). Eigenvectors were selected iteratively according to model performance (indicated by Akaike information criterion) and the degree of reduction in spatial autocorrelation (Dormann et al., 2007). In order to have only a low number of explanatory variables, hierarchical partitioning was applied to residuals of linear models of spatial eigenvectors and response variables. In this way, we were able discern the net effects of variables without spatial autocorrelation.

Statistical analyses were performed using the R statistical software (R Development Core Team, 2006) and SAM (Rangel et al., 2010) for the spatial autocorrelation measurements.

Results

OVERALL SHIFTS OF THE ALPINE TREELINE ECOTONE

In both regions, an overall advance of the alpine treeline ecotone was observed over the whole study period (1936–2005 for GM and 1953–2005 for HJ; Table 2, Fig. 3). Assuming linear shifts, the upward advance of the timberline ranged from 0.30 m yr^{-1} in HJ to 0.43 m yr^{-1} in GM. The overall upward shift of the treeline ranged from 0.26 m yr^{-1} in GM to 0.28 m yr^{-1} in HJ. Advances of the timberline and treeline were more intensive in the first part of the study period in both regions (Table 2). Afterwards, the treeline ecotone upward shift became slower, and in HJ, even a slight recession of timberline was observed. Although the highest elevation of treeline continuously increased in GM, the treeline

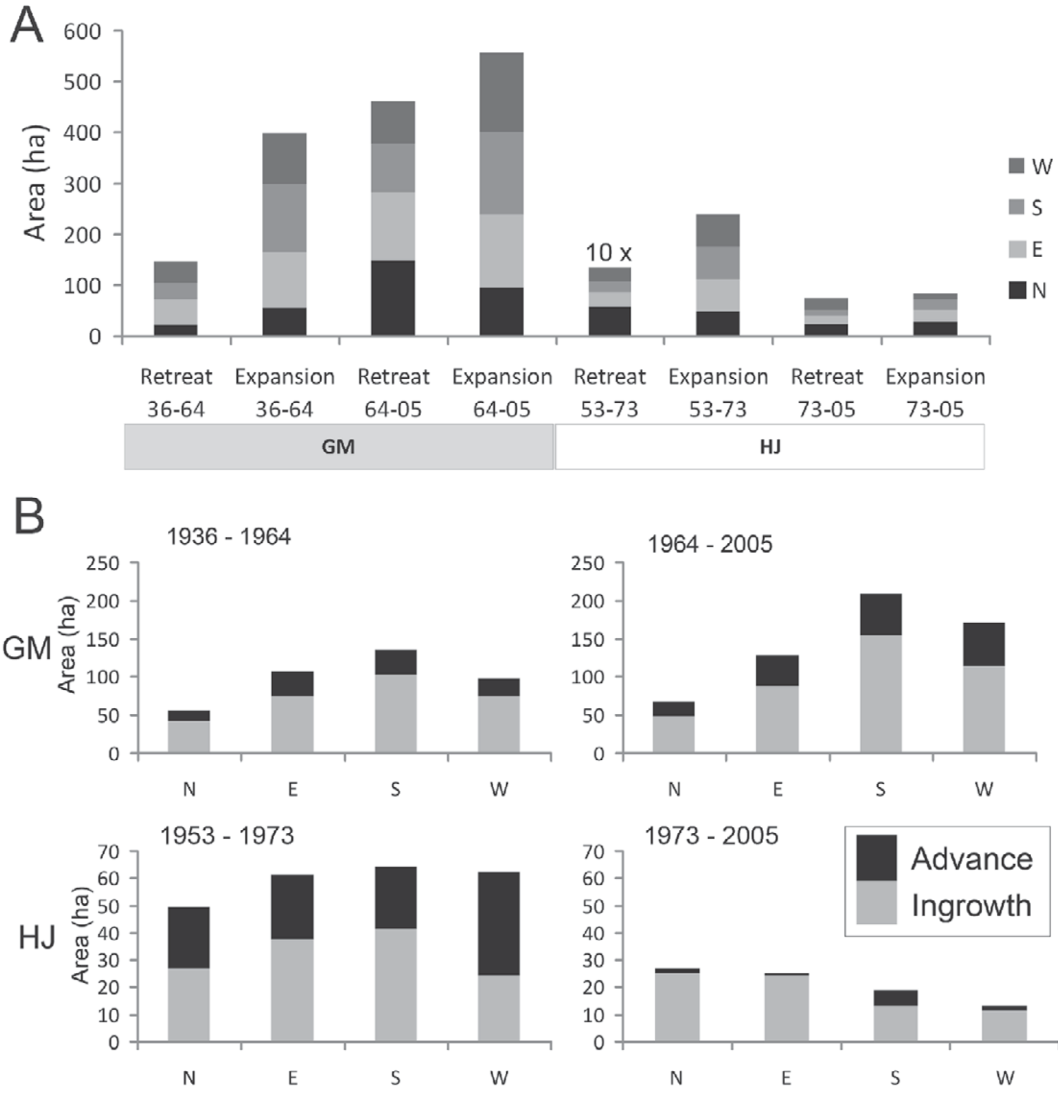

FIGURE 3. (A) Areal extent of retreats and expansions of timberline, corrected for tectonic bias. Note that "Retreat 53-73" in HJ is magnified by a factor of 10. (B) Areas (corrected for tectonic bias) of timberline expansion showing contributions from advances and ingrowth.

maximum position in HJ was nearly stable over the entire period. In both GM and HJ, and over both parts of the study period, the maximum advances, both in terms of timberline altitude increase and area of advance, occurred on slopes of all aspects except north-facing slopes (Fig. 3, part A). On north-facing slopes, the altitudinal and areal increases of forested patches were the smallest, and the largest area with decreasing timberline was found there. During the first part of the study period, the treeline altitudinal increase was most pronounced on east-facing slopes, whereas no prevailing aspect-related tendency was observed in the second part of the study period. Over the entire study period, and for both regions, areas of timberline expansion were more extensive than areas of recession; however, this difference was markedly greater in the first part of the study period (Fig. 3, part A).

The increased area of forest patches was mostly represented by ingrowth (70% in GM and 55%–88 % in HJ, Fig. 3, part B). Advances of the timberline above the treeline (i.e., "real" advances) were highly represented in the first part of the study period in HJ (45% of total increase in area), but much less so during the second part of study period (only 12% of total increase in area). Except for south-facing slopes, almost no real advances of the timberline occurred in HJ over the 1973–2005 period.

SPATIAL PATTERNS

Local Moran's I of model residuals were usually low (always lower than 0.15), but in some cases (GM 1936–1964 both including and excluding spruce cover, HJ 1953–1973, and HJ 1973–2005 excluding spruce cover), these values significantly differed from a random pattern ($p < 0.05$). For timberline advances, only the net effects of variables after spatial autocorrelation has been filtered out are presented here.

In both areas and in all studied periods, initial spruce cover was the explanatory variable with the highest explanatory power (from 32% in GM 1964–2005 to 90% in HJ 1953–1973), and the explained deviances of models including initial spruce cover were rather high (between 15% in GM 1964–2005 and 60% in HJ 1953–1973) (Fig. 4).

After the effect of initial spruce cover was filtered out, in GM (Fig. 5, part A), timberline advance was more probable on warm (south-facing) sites with low altitude. In addition, low values of dwarf-pine cover, well-dispersed trees, and, only in 1936–1964 small tree size, were site characteristics that made timberline advance more probable. Generally in GM, the effect of vegetation-structure variables was stronger than the effect of topographic variables (Fig.

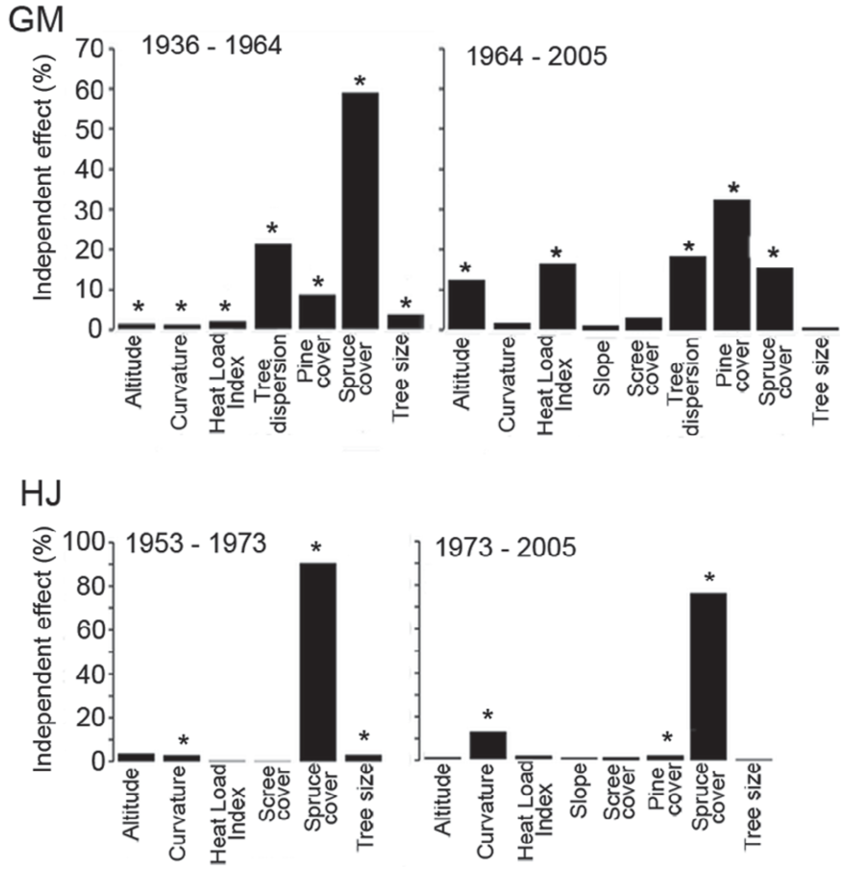

FIGURE 4. Independent effects of individual variables including spruce cover revealed by hierarchical partitioning within logistic regression framework. * Indicates significant results at probability level p < 0.05.

5, part A). Linear models were statistically significant and explained 12% (GM 1936–1964) and 17% (GM 1964–2005) of variance.

In the early and late parts of the study period in HJ (Fig. 5, part B), after the spruce cover effect was filtered out, altitude, curvature, and tree dispersion significantly influenced timberline advance, which preferentially occurred at low altitudes, on convex slopes and on sites with well-dispersed trees. Between 1953 and 1973, timberline upward shift also occurred at sites with small trees (Fig. 5, part B). Linear models were statistically significant and explained 6% (1953–1973) and 11% (1973–2005) of data variance, respectively.

The effects of vegetation structure and topographic variables on timberline upward shifts differed among plots, based upon their initial spruce coverage (Fig. 5). In GM, in the 1936–1964 period, the effects of both tree dispersion and dwarf pine cover increased gradually with increasing initial spruce cover. In contrast, at sample plots with high levels of original spruce cover, the influence of topographic variables (altitude, heat load) and tree size decreased (Fig. 5). In GM, in the period 1964–2005, the independent effects of topographic variables (altitude and heat load) were smallest on plots with the greatest initial cover of spruce stands. In contrast, significant vegetation structure variables (tree dispersion and dwarf pine cover) had their weakest effects on plots with the lowest initial cover of spruce and greatest effects on plots with high initial cover of spruce. The overall explained variability as indicated by R^2 was either stable in the 1936 to 1964 period (16%–17%) or the decreasing with increasing initial spruce cover in the 1964–2005 period (from 22% to 6%). In the last case (plots with spruce cover greater than 25%), the model was not statistically significant ($p = 0.10$).

In HJ, over the first part of the study period, the separate analysis for sample plots categorized by original spruce cover was limited to the category with spruce cover up to 15%, as there were too few sample plots in the remaining two categories. At sample plots with less than 15% spruce cover, only topographic variables such as altitude and curvature significantly affected timberline upward shift (Fig. 5), in contrast to the entire set of sample plots, which displayed significant effects of tree dispersion and tree size. The linear model was significant, but with low explanatory power ($R^2 = 0.06$).

In HJ, in the second part of the study period (1971–2005), due to the limited number of sample plots with spruce cover above 25%, only the sample plots in the up-to 15% and 15%–25% original spruce cover categories were analyzed. On plots with original spruce cover lower than 15%, timberline upward shifts were more probable at sites on low-curvature (i.e., concave) slopes, south-facing slopes, and sites with well-dispersed trees. On plots with 15%–25% original spruce cover, the effect of tree dispersion increased, and the effects of significant topographic variables either decreased (altitude, heat load) or increased (slope) in comparison to sample plots with lower initial spruce cover. Linear models accounted for 19% (1953–1973) or 25% (1973–2005) variance explained, respectively.

The scarcity of sample plots that experienced retreats during the first part of the study periods (<22 in each region) did not permit statistical analysis involving these areas. Over the second part of the study period in GM, the timberline retreats were more probable at high elevations and on north-facing slopes (Fig. 6, part A).The model was statistically significant and accounted for 38% of deviance. In HJ, convex parts of the terrain and less-inclined slopes had significantly greater probabilities of forest retreat (Fig.

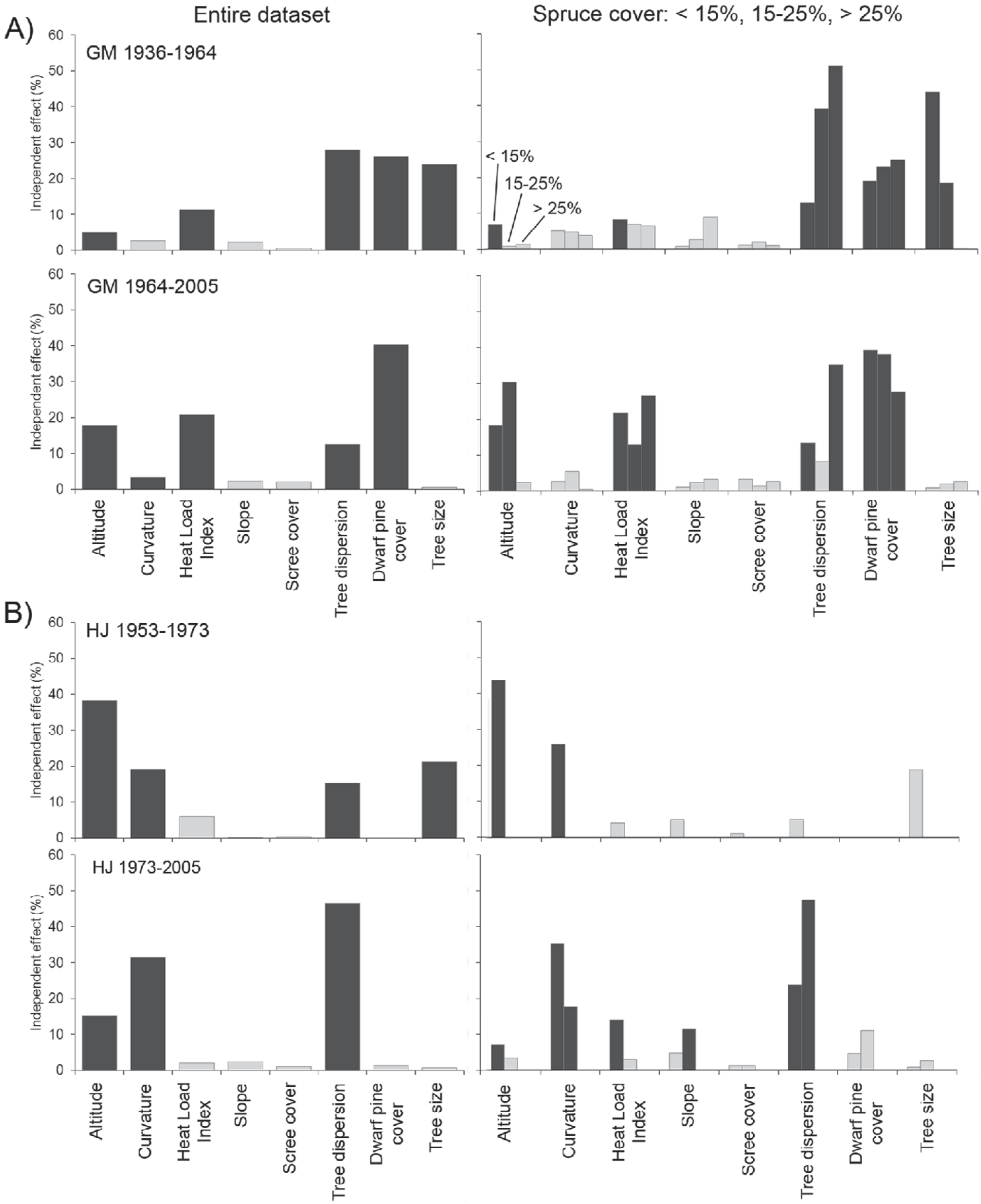

FIGURE 5 Independent effects of individual variables after the effect of initial spruce cover was filtered out. Hierarchical partitioning within linear regression was performed for entire data set and for sample plots categorized by their initial spruce cover. Black columns indicate significant effect at probability level $p < 0.05$. (A) Giant Mountains; (B) Hrubý Jeseník Mountains.

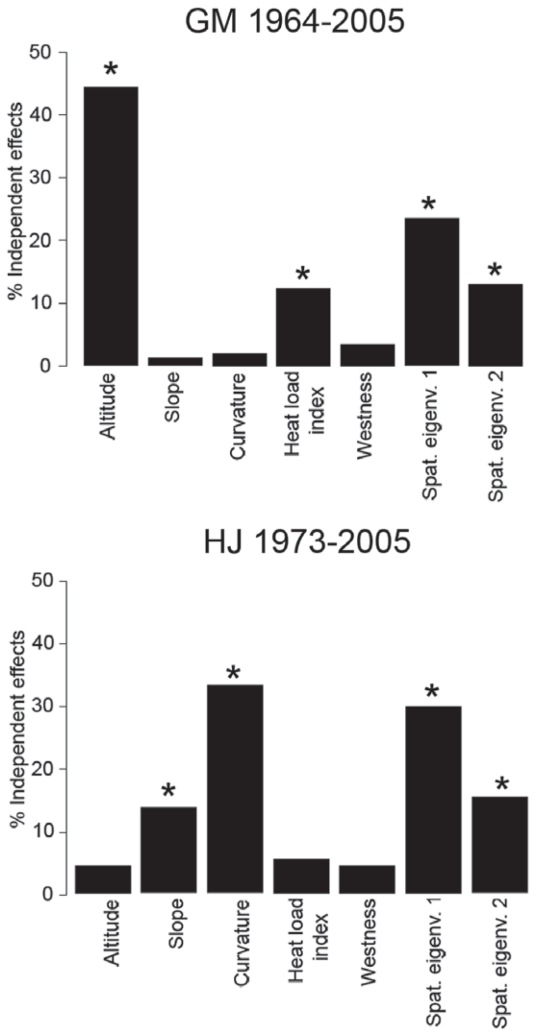

FIGURE 6. Independent effects of individual variables on probability of timberline retreat as indicated by hierarchical partitioning within logistic regression framework. * Indicates significant results at probability level p < 0.05.

6, part B). The logistic model was statistically significant and explained 13% of deviance. Because the sample plots with timberline retreats were concentrated in a few locations, the effects of spatial autocorrelation were rather high.

Discussion

SPATIAL PATTERNS OF TREELINE ECOTONE SHIFTS

Over the past 80 years, the studied area was subjected to a temperature increase of approximately 1 °C (Głowicki, 1998) and the cessation of mountain agriculture (Lokvenc, 1995), resulting in the extensive upward advance of tree stands. The dominant portion of tree stand expansion was represented by forest infilling of treeless areas below the original position of the alpine treeline. Similar patterns of forest upward advances have been reported from the Alps and Pyrenees (Gehrig-Fasel et al., 2007; Améztegui et al., 2010). The dominance of densification over real advances of the alpine treeline suggests that the expansion of tree stands is affected by positive feedback (Elliot, 2011) and probably by the distance that the seeds can be dispersed (compare with Wallentin et al., 2008). Moreover, this expansion is often into bay-like, downward outposts of tundra that can be colonized by tree stands spreading both upward from the bottom and horizontally from the sides. This simple geometric mechanism allows the rapid closing of forest-free patches in lower parts of the alpine treeline ecotone. In addition, tree establishment above depressed timberlines is expected to be more rapid because these sites are less temperature-limited in comparison with upper parts of the alpine treeline ecotone (Weisberg et al., 2013).

We found that the advance of tree stands showed a pronounced spatial pattern affected mainly by vegetation-structure variables (particularly original tree cover) and to some extent by topographic variables. The high importance of initial tree cover for timberline advance was not surprising considering the methodological approach used—the higher initial tree coverage requires smaller gains to achieve coverage that can be classified as forest. If only the net effect of topographic and vegetation-structure variables without the effect of initial tree cover is considered, both low elevations and south-facing slopes, that is, warmer environments, were favored for timberline upward shifts. Examining the effects of biotic variables, timberline upward shifts were typical for sites (i) with well-dispersed trees and (ii) with low cover of dwarf-pine. In cold environments, clustered trees often indicate stressful environmental conditions (Elliot, 2011) with a lower potential for quick expansion. Particularly in the GM, forest expanded on sites with available space for spruce expansion, as indicated by low proportion of dwarf pine cover. We suggest that in GM the extensive dwarf pine presence was the limiting factor of forest expansion, largely explaining the markedly smaller upward shift of the treeline ecotone (in terms of both timberline and treeline) there in comparison to HJ during the first part of the study period, as the latter range lacked extensive dwarf pine stands. This finding suggests that the competition between prostrate shrubs and trees might more generally play an important role in inhibiting forest expansion, especially on sites where the prostrate shrub cover is high (Anthelme et al., 2003; Dullinger et al., 2003; Šenfeldr et al., 2014).

In both of the ranges, in the early part of the study period, a significant role was also played by tree size (in terms of mean basal projection of crown). We suggest that relatively numerous small trees helped the forest expand by increasing tree cover through growth. In addition, small trees might simply indicate sites undergoing rapid forest expansion.

The effects of both biotic and topographic variables on the upward expansion of tree stands were not, however, consistent throughout the dynamic process of treeline ecotone advance. Instead, we found that changing tree coverage was associated with changes in the effects of environmental and biotic variables. Altitude and heat load were important mainly when the original spruce cover was low; in contrast, the relative importance of biotic factors such as dwarf pine stand cover and tree dispersion increased when initial tree cover was high. The increased importance of topographic factors at low tree-stand cover probably resulted from weak positive feedback (Stueve et al., 2009). Small trees and low numbers of trees are not capable of effectively influencing site environmental conditions in terms of ground temperatures and wind speeds (Alftine and Malanson, 2004; Malanson et al., 2007). As soon as the positive feedback is strong enough due to increasing canopy cover, the effect of topographic variables probably decreases (compare with Li and Yang, 2004; Barbeito et al., 2012).

TABLE 3

Rates of treeline ecotone upward shift in European mountains. Temperature increase (last column) represents slope of the linear fit of mean winter (DJF) and summer (JJA) temperatures over 1902–2009 period. Temperatures were derived from upgraded CRU TS data set (Mitchell and Jones, 2005).

Region	Coordinates	Treeline altitude (m a.s.l.)	Treeline upward advance (m yr^{-1})	Temperature increase
Giant Mountains	50°01′N 17°36′E	1320	0.43 (1936–2005)	+0.012 W +0.008 S
Hrubý Jeseník Mountains	50°43′N 15°40′E	1330	0.30 (1953–2005)	+0.006 W +0.001 S
Polar Ural (Shiyatov et al., 2007)	66°49′N 65°35′E	250	0.33 (1910–2000)	+0.000 W +0.005 S
Southern Ural (Kammer et al., 2009)	54°32′N 58°51′E	1300	1.14 (1929–2000)	+0.025 W +0.006 S
Khibiny Mountains (Mathisen et al., 2014)	68°00′N 35° 00′E	500	0.55 (1958–2008)	+0.006 W +0.004 S
Northern Fenoscandia (Sutinen et al., 2012)	68°00′N 24°09′E	500	0.62 (1947–2003)	–0.001 W +0.009 S
Northern Scandes – Abisko (Van Bogaert et al., 2011)	68°30′N 19°00′E	700	0.2 (1912–2009)	+0.003 W +0.011 S
Swedish Scandes (Kullman and Oberg, 2009)	62°00′N 12°30′E	~900	0.74–0.98 (1915–2007)	+0.008 W +0.008 S
Italian Alps–Val Massino (Sondrio) (Díaz-Varela et al., 2010)	46°13′N 9°38′E	1950	1.30 (1957–2003)	+0.012 W +0.014 S
Italian Alps–Valle d'Aosta (Leonelli et al., 2011)	45°47′N 7°21′E	2500	1.06 (1901–2008)	+0.011 W +0.014 S
Ukrainian Carpathians (Martazinova et al., 2011)	48°00′N 23°00′E	~1400	0.50 (1930–2000)	+0.005 W +0.000 S
Romanian Carpathians (Kern and Popa, 2008)	47°06′N 25°12′E	1800	0.67 (1906–2006)	+0.009 W +0.006 S

Temporal changes in the significance of certain variables between the early and late part of the study period were also attributed to the changing position of the timberline. In particular, new timberline position in complex topography would have led to changes in effects of topographical variables. For example, a significant increase in areas of ingrowths occurred in HJ during the second part of the study period (1973–2005), during which terrain curvature had its most significant effect on timberline expansion there. We suggest that tree stands expanded upward until reaching the convex margins of summit flats, which are characterized by high climatic stress (wind abrasion, extremely low or high snow depth on windward or leeward sides, and deep freezing of soils), as suggested by, for example, Dalen and Hofgaard (2005) and Kullman (2005). These unfavorable sites probably slowed the upward expansion of tree stands, resulting in larger proportions of the advances being represented by ingrowth. On the other hand, the proportion of real advances in the first part of the study period was significantly higher in HJ than in GM, which might have resulted from the overall more depressed timberline in HJ, due to past human activities in this area (Treml and Banaš, 2000).

The negative effects of extensive shrub cover and convex slopes on timberline upward shift are in sharp contrast with the opposite findings of Weisberg et al. (2013) from the geographically close area of the Carpathians. We suggest that the differences in these findings might be attributable to more intense wind action in the Sudetes than in the Carpathians. The Sudetes are among the windiest locations of European mountains (Jeník, 1961; Migala, 2005), and in highly windy conditions, the convex parts of terrain

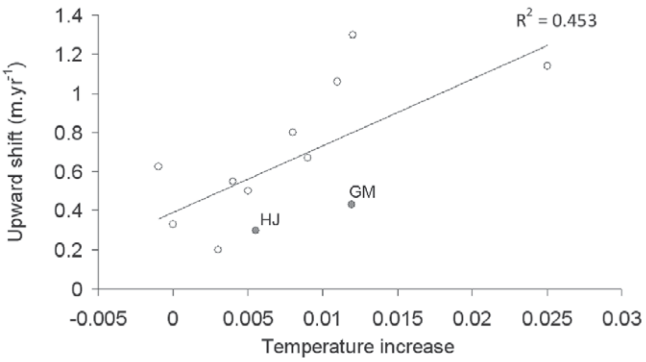

FIGURE 7. Relationship between average annual rate of treeline shift and winter temperature increase (data from Table 3). Temperature increase represents slope of the linear fit of mean winter (DJF) temperatures over the 1902–2009 period.

are generally less suitable for tree establishment and survival (Kullman, 2005). Furthermore, at wind-affected treelines, shrubs are probably more competitive than trees (Takahashi, 2014; Šenfeldr et al., 2014), and their competitive effects might outweigh facilitation of tree establishment and tree growth at early ontogenetic stages (Callaway et al., 2002).

Our data also show that similar variables to those limiting expansion play a role in forcing timberline retreat. High altitudes, convex parts of terrain, and cold (e.g., north-facing) slopes were prone to forest retreat or only limited advance in the Sudetes. Sites that are relatively more climatically stressed by low temperature, extremely high or low snow pack, or high wind abrasion (Kullman, 2007; Kajimoto et al., 2002) have a higher probability of forest retreat. The first-order driver of forest retreat was likely acid pollution in the 1970s and 1980s (Kroupová, 2002), but its influence was stronger on climatically stressed stands.

REGIONAL COMPARISON IN TREELINE DYNAMICS

Comparing our data on Sudetes treeline shifts with similarly defined treelines in other European mountains (Table 3) invites inquiry into the regional differences among these dynamics. Treeline ecotone advances in HJ and GM (in terms of timberline) were lesser than those in most of the other mountain areas. Our overview (Table 3) supports the inference of Harsch et al. (2009) that winter temperatures are more indicative than other seasonal temperatures for treeline advances. Thus, we found treeline ecotone advance to have higher Pearson correlations with winter than summer temperature trends (*r winter* = 0.68, *r summer* = 0.31). If the upward shifts listed in Table 3 are examined in relation to winter temperature increases, Sudetes treelines are situated below the trend line, indicating lower values of upward shifts than expected (Fig. 7). Local characteristics of HJ and GM may be at least partly responsible for the relatively small upward shifts detected in these areas. Their treeline ecotones are situated below the convex edges of summit plateaus and are therefore strongly affected by wind and snow redistribution (compare with Kullman, 2005). Furthermore, the competition with closed dwarf pine stands has slowed the upward expansion of trees. Convex parts of slopes and the presence of prostrate shrubs as second-order factors of treeline position probably affect treeline dynamics in many mountain regions, especially in those under influence of intense wind action (e.g., Kullman, 2007). Additionally, in the Sudetes, the period of acid pollution in the 1970s and 1980s likely slowed or even negated upward forest advance for some time. The variability unexplained by winter temperatures in Figure 7 might be attributed to differences in treeline characteristics and to the methodologies that have been used to delineate them.

Conclusions

The alpine timberline in the Sudetes showed an average annual upward advance of 0.43 m since 1936 in the Giant Mountains and 0.30 m since 1953 in the Hrubý Jeseník Mountains. In the landscape-scale context, treeline ecotone advance showed great spatial and temporal variability attributed mainly to vegetation-structure variables and terrain properties. The dominant process associated with the upward advance of alpine timberline was the densification of the lower part of the treeline ecotone. The most important predictors of forest advance were tree presence and dispersion. Topographic variables, including altitude and aspect-related heat load, were important mainly at sites with sparse tree stands, probably due to low positive feedback associated with scattered trees. If, however, the original tree cover was high, the effect of terrain variables decreased and the probability of forest advance increased with increasing tree dispersion and decreasing cover of prostrate dwarf pine stands. High cover of prostrate dwarf pine shrubs and the presence of convex parts of slopes with extreme microclimatic conditions seem to have been important constraints on forest advance at wind-affected treelines typical of the Sudetes. The effects of these two characteristics probably contributed to the relatively small upward advance of the treeline ecotone in the Sudetes Mountains compared with other European mountain ranges. As second-order factors, topographic and vegetation-structure variables may explain differences in treeline warming responses among mountain landscapes in different regions.

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APPENDIX

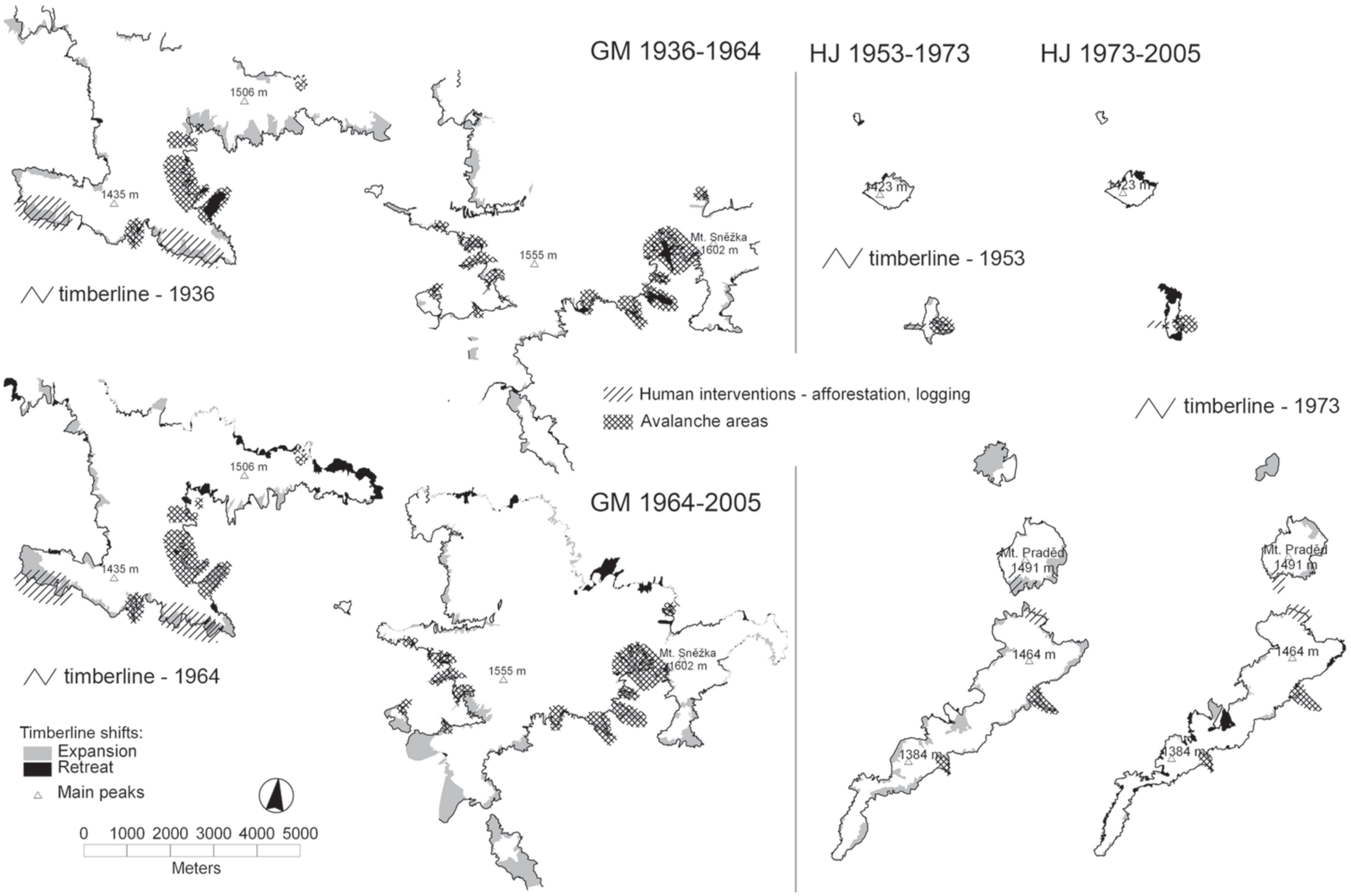

FIGURE A1. Extent of timberline shifts in the Sudetes. Only sections of timberline with data accessible from all periods are shown. This part of timberline was therefore used for comparisons of timberline and treeline altitudes.