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Landscape Influences on Recent Timberline Shifts in the Carpathian Mountains: Abiotic Influences Modulate Effects of Land-Use Change

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Abstract

Expected shifts in the upper forest limit of many mountain ranges due to anthropogenic climate change will likely be constrained by current and historical land-use practices. We used historical maps and Landsat satellite imagery to analyze timberline change for the entire Carpathian range in Eastern Europe. Our objectives were (1) to compare 19th and 20th century timberline elevations across regions differing in sociopolitical history and land-use trends; and (2) to quantify how land-use patterns and environmental influences were associated with changes in timberline position. Timberline changes across geopolitical regions were consistent with regional variations in re-settlement rates and population shifts following World War II. Important predictors for timberline rise were the mainly biophysical factors of slope steepness, timberline elevation, shrub cover, topographic curvature, aspect, and proximity to roads. For horizontal migration, important predictors were proximity to shepherd's huts, elevation, population density, forest composition, and shrub cover. Overall, cultural influences were critical for understanding the response of Carpathian timberlines to global change, yet biophysical influences proved important where reforestation was already occurring. In mountain ranges with prevalent agricultural abandonment, forest migration associated with climate warming may lead to increased contrast in the forest-alpine ecotone between areas with and without intensive land-use.

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Introduction

Globally, mountain treeline is expected to rise in elevation with climate warming, and recent treeline shifts have been attributed to climate change (e.g. Harsch et al., 2009). The expected climate change response is overlaid on a backdrop of changing land-use patterns. For many of Europe's mountain ranges, the Industrial Revolution has led to agricultural abandonment, resulting in forest expansion, while there is continued intensive land-use in other parts. For examples, in the Swiss Alps a trend toward increasing forest area, dubbed the forest transition, has been evident since the 1850s (Mather and Fairbairn, 2000), as is the case in the Orawa region in Poland (Kozak, 2003), while in western Ukraine a clear trend has become evident only since World War II (WWII) (Kuemmerle et al., 2011). Forest cover change trends for elevations above 1000 m have differed across regions of the Carpathians over 1880–2000, with a clear forest cover increase only on Slovak and Polish territory, and a decreasing or stable forest cover in Ukraine and North and South Romania (Shandra et al., 2013).

Understanding legacy effects of past changes and constraints imposed by ongoing land-use practices will help us to better predict future response of mountain forests. Significant increases in forest elevation observed in major European mountain ranges have been attributed primarily to land-use change (Gehrig-Fasel et al., 2007). However, many researchers have observed that because agricultural abandonment and reduced grazing pressure occurred synchronously with climate warming following the Little Ice Age, it may not be possible to distinguish climate warming and land-use change as causal factors (Motta and Nola, 2001; Mihai et al., 2007). Thus, the two types of causes, climate warming and land-use change, must be considered simultaneously in order to forecast future change to timberline position and structure of the forest-tundra ecotone. In many European mountains treeline response to agricultural abandonment can only happen if climate is favorable for tree establishment at higher elevations. Similarly, treeline response to climate change can only occur if land uses are favorable for tree establishment and range expansion.

We used historical maps and survey information in combination with satellite imagery from recent decades to analyze timberline change for the entire Carpathian mountain range. We define ''timberline'' as the upper elevational limit of closed-canopy forest as differentiated from aerial observations or satellite imagery. Historical maps have been widely used for land cover change research previously, but at regional scales (Kozak, 2003; Kricsfalusy et al., 2008); satellite imagery has been widely utilized for vegetation change studies in the Carpathian region (e.g. Dezso et al., 2005; Mihai et al., 2007; Kuemmerle et al., 2009). Timberline change was analyzed in lieu of treeline change (defined as the upper elevational limit of tree species regardless of growth form) because the location of timberline was more easily reconstructed from archival maps and satellite imagery than the treeline ecotone, which is considerably less distinct. We separately considered timberline elevational rise and the horizontal movement of timberline as distinct response variables that might differ in their relationships with envi-

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ronmental and sociopolitical influences. We expect elevational rise to be more sensitive to biophysical constraints on plant establishment and growth, and horizontal movement to be more sensitive to land-use influences.

Our objectives were to: (1) compare timberline elevations from 1880 to 1930 and from 1930 to 2000 across multiple geographic regions differing in sociopolitical history and land-use trends; and (2) quantify how land-use patterns and environmental influences were associated with changes in timberline position from 1930 to 2000. The earlier time period was not selected for this second analysis because of the relatively coarse resolution and reduced accuracy associated with the 1880 map. We hypothesized that land-use influences and topographic variables associated with climate have interacted to control the spatial variability in timberline migration. We predicted that after controlling statistically for the effects of other topographic and land-use variables, there would be an inverse relationship between the rate of timberline rise and elevation of the timberline. Our rationale was that areas where timberline has been depressed the most by mountain agriculture should be at lower elevations closer to the thermal optima of the dominant tree species, allowing timberline to rise through tree migration processes more rapidly following agricultural abandonment.

Methods

STUDY AREA

The study area included the entire portion of the Carpathian Mountains above 1000 m in elevation for which accurate historical data (1880–2000) were available, comprising an area of 23,261 km^2. The total area of locations which were considered to be inaccurate on old maps, based on timberline elevations that exceeded an inferred climatic threshold (Shandra et al., 2013) and where the mapped timberline appeared to correspond to extant shrub vegetation, occupies 1.1% of the study area. Today, the study area includes portions of Poland, Slovakia, Ukraine, and Romania, although geopolitical boundaries have varied over the period of study. Our analysis considered four regions that integrated political, physiographic, and climatic considerations: West Carpathians (Poland and Slovakia), Ukrainian Carpathians (Eastern Carpathians in Ukraine), North Romanian Carpathians (Bihor massif and Romanian part of Eastern Carpathians), and South Carpathians (Fig. 1). Two main types of timberline are present—a deciduous timberline forest dominated by European beech (*Fagus sylvatica*), and a coniferous timberline dominated by Norway spruce (*Picea abies*) with stone pine (*Pinus cembra*) as a lesser component. Above the coniferous timberline, prostrate forms of mountain pine (*Pinus mugo*), dwarf juniper (*Juniperus communis*), and green alder (*Alnus viridis*) often form dense thickets. The deciduous timberline is predominantly of anthropogenic origin, resulting from removal of coniferous forests at higher elevation (Komendar, 1966).

TIMBERLINE RECONSTRUCTIONS FROM HISTORICAL MAPS

Historical timberline position from the late 1880s was reconstructed as depicted on topographic maps from the Third Military Survey of the Austro-Hungarian Empire, covering the whole study

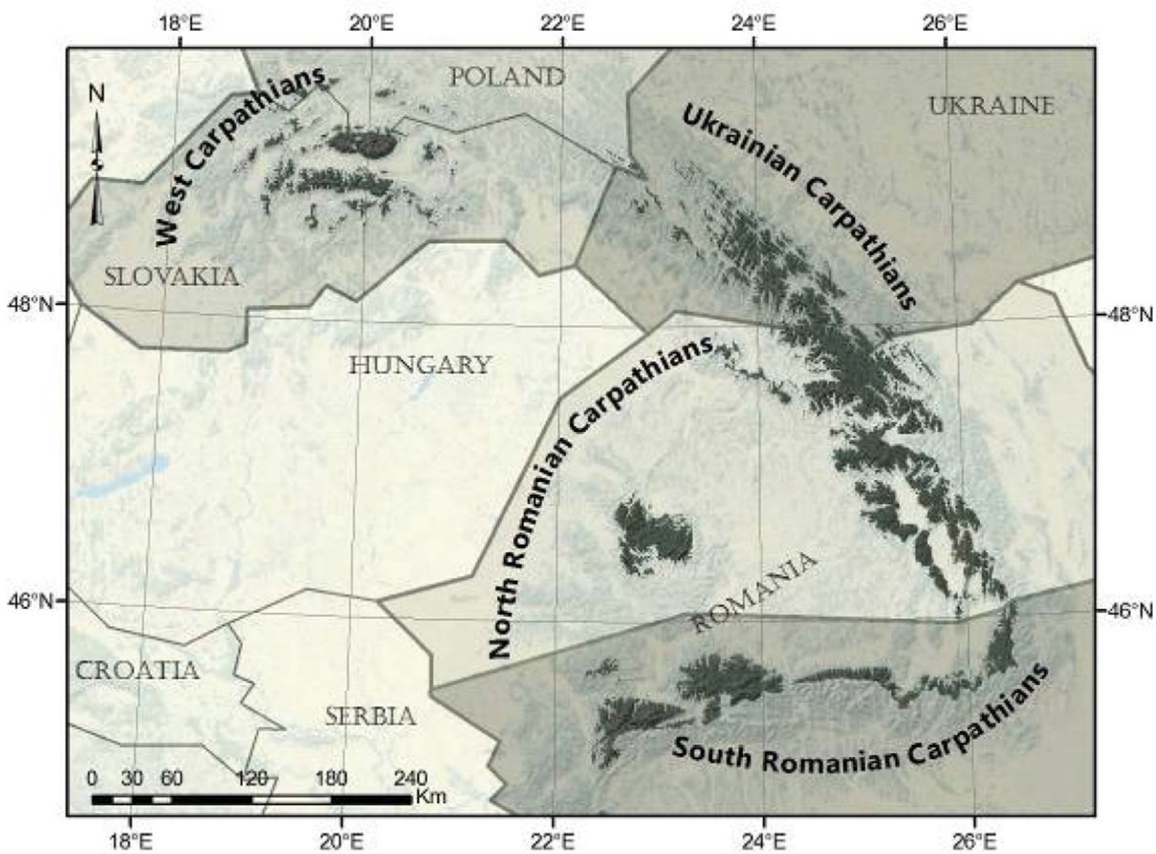

FIGURE 1. Map of the study region. Area within which timberline change was studied (with elevations over 1000 m) is shaded dark gray.

region at the scale 1:75,000. Timberline position during the 1930s was reconstructed using a series of topographic maps issued in the period between WWI and WWII: revised maps of the Third Military Survey (Slovakian and Ukrainian territory, 1930s, 1:75,000), WIG maps (Polish and Ukrainian territory, 1930s, 1:100,000), and Planurile Directoare de Tragere maps (Romania, 1920s, 1:20,000). Digital map sheets (137 from 1880 and 279 from 1930) were georeferenced using ground control points (GCPs) and mosaicked. Projection parameters of the Third Military Survey (1880) varied from sheet to sheet, requiring that a substitute sinusoid projection be used for each map column, making it possible to follow the original map trapezoid shape with an accuracy of approximately 20 m (Molnár and Timár, 2009). Instead of rectifying each column in a separate projection, we used a single Albers conic projection with a WGS84 datum for our study area, giving us a comparable error of approximately 25 m. The same procedure was carried out for maps of the 1930 time period. A third order polynomial function was used for georeferencing based on GCPs from 1:100,000 Soviet military topographic maps and tourist maps of the Slovak Republic. The average root mean squared (RMS) error for all sheets was 74 m, after omission of certain areas (mainly in Romania) that had lowest geodetical accuracy.

To delineate timberline, we first digitized a vector layer of non-forested territory by on-screen digitizing from the historical maps. From this layer, we identified timberlines as continuous lines separating forest from non-forested land. Highly interrupted segments (<200 m) were excluded, as were small forested patches above timberline (typically <1 ha).

TIMBERLINE CLASSIFICATION FROM LANDSAT IMAGERY

The modern Carpathian timberline was delineated using 13 Landsat Enhanced Thematic Mapper (ETM) scenes, acquired between 2000 and 2002 during the summer months (May–August). Atmospheric correction was performed using the dark object subtraction method for separate scenes that were then mosaicked and registered to modern topographic maps. For topographic correction, which can be a problem for image analysis of mountain territories, we used a combination of parametric and non-parametric methods to adjust brightness values of the image mosaic based on a hillshade image generated from the SRTM digital elevation model (DEM) data set and acquisition time of separate images. Supervised maximum likelihood classification was used to distinguish eight land cover types based on training data from field observations and high-resolution Google Earth imagery and photographs. Land cover types included: deciduous and coniferous forest; lakes; shrubs; grassland and pasture; recently logged; and rocks. Overall classification accuracy was 78%. Due to a high rate of misclassification between coniferous forest and high-elevation shrub communities, manual delineation of timberline from photo-interpretation of Google Earth high-resolution imagery was used to improve the automatic classification in problem areas. This post-processing step made use of the Tiles-on-Line instrument (Mitrich tools, http://mitrichtools.narod.ru/Eng/TilesOnLine eng.htm). The overall classification accuracy of the corrected classification was 88%, with a binary forest–non-forest classification accuracy of 96%. A vector layer of treeless area was created from this binary classification, comparable to the vector layer from the old topographic maps. Image processing analysis was conducted in Envi 4.7 and ArcGIS 9.3 software.

PREDICTOR VARIABLES

To differentiate the relative importance of land-use change and environmental influences for recent timberline dynamics in the Carpathian Mountains, we considered topographic, biotic, and cultural sets of predictor variables. Topographic variables, including elevation (m), slope steepness (percent), northness, and curvature, were derived using ArcGIS 9.3 software from an SRTM DEM at 90 m resolution obtained through the CGIAR geoportal (http://srtm.csi.cgiar.org; accessed 17 October 2009). The northness index uses a cosine transformation to linearize slope aspect values such that north-facing slopes have the maximum value of one, and south-facing slopes have the minimum value of zero. The curvature index describes the second derivative of the slope for a nine-cell neighborhood, with positive values indicating upward convexity, negative values indicating upward concavity, and zero values indicating a flat surface. Biotic variables, including vegetation cover of coniferous forest (mainly *Picea abies*), deciduous forest (mainly *Fagus sylvatica*), recently logged forest, shrubs, grass or pasture, and rocks, were derived from the maximum likelihood classification of 2000–2002 Landsat imagery (described above). Cultural variables included the four geopolitical regions already described, distance to the nearest shed or shepherd's hut (km; digitized from historical topographic maps dating from 1890–1940), distance to the nearest primary road (km), distance to the nearest highway (km), density of residential areas (km^{-2}), density of railroads ($km\ km^{-2}$), and population density (km^{-2}). Population density for 2000 was obtained from the Global Rural-Urban Mapping Project (CIESIN, 2005); road, railroad, and settlement shapefiles were downloaded from http://mapcruzin.com; shepherd's huts were digitized from historical maps.

DATA ANALYSIS

Timberline change was quantified in two ways: (1) as the elevational difference (ED) between timberline position in the year 2000 and the year 1930, and (2) as the horizontal distance (HD) between timberline position in the two years. To calculate both measures, 1792 sample points were first generated along the 2000 timberline at regular intervals of 200 m. For each point, geographic coordinates were recorded for the nearest positions on the historical timberlines. Elevational distance was calculated as the difference between elevations of pairs of nearest points between years, and horizontal distance was calculated as the Euclidean, planar distance between the points.

For regional comparisons of elevational timberline shifts, occurrences of timberline rise, decline, and lack of change were identified by comparing the reconstructed elevation of timberline for each of the three time periods (1880, 1930, 2000), and tallied according to geopolitical region separately for the two time intervals (1880–1930, 1930–2000). The chi-square test of association was applied to the resulting contingency table of counts for the different kinds of timberline change, to test the hypothesis that different kinds of timberline change were associated more with certain geographic regions than would be expected given a random process.

Regional differences were then explored graphically as the proportion of timberline segments that experienced rise, decline, or no detectable change for each region during the two time periods. Because a 90 m digital elevation model was used to quantify the elevational change of timberline, small shifts in timberline position (occurring within a mean horizontal distance of 90 m) would not have registered reliably as elevational shifts (i.e. timberline would still be located within the same pixel on the elevation raster as during the previous time period).

For statistical modeling of the importance of land-use patterns and environmental influences, we restricted our analysis to areas where land abandonment had likely occurred or where there was potential for timberline to respond to climate change, as indicated by timberline movement. Thus we only included in this analysis those places where timberline had been documented to rise between the two time periods ($n = 871$ intervals of 200 m timberline length).

Boosted regression tree (BRT) analysis was used to quantify associations between the predictor variables and historical timberline rise as ED and HD. Regression tree analysis provides predictive, dichotomous decision trees where data are split iteratively into increasingly homogeneous groups, and allows for nonlinear functional relationships as well as modeling hierarchical interactive effects (De'ath and Fabricius, 2000). BRT analysis is a machine learning method that uses randomization to generate a collection of regression tree models, improving model stability and prediction ability (De'ath, 2007; Elith et al., 2008). The BRT approach provides an unbiased ranking of the relative importance of predictor variables as well as partial dependence plots describing relationships between predictor and response variables after accounting for the average effects of other predictor variables (Elith et al., 2008). Relative importance is calculated as the number of times a variable is selected as a node weighed by the squared improvement to the regression tree model as a result of including that node across all trees, and can be interpreted as the relative amount of variance explained by the variable (Elith et al., 2008). BRT analysis also ranks interactions among variables in order of their importance. Based upon this ranking, we explored interactions graphically using perspective plots.

The BRT analyses assumed a Gaussian distribution of response variables, and were implemented using the *gbm.step* function in the *dismo* package (Hijmans et al., 2012) of the statistical program R 2.15.0 (R Development Core Team, 2012; http://www.r-project.org). This function allows users to vary the learning rate (*lr*), tree complexity (*tc*), and bag fraction (i.e. proportion of observations withheld for testing each tree iteration in a tenfold cross-validation process). We fixed the bag fraction at 0.5 and chose *lr* and *tc* parameters that minimized the cross-validated, residual deviance after exploring the ranges of *lr* (0.0001 to 0.1) and *tc* (2 to 15) suggested by Elith et al. (2008). Parameters selected for modeling ED timberline change were $lr = 0.005$, $tc = 7$, resulting in 1150 trees used to fit the final model. Parameters selected for modeling HD timberline change were $lr = 0.0002$, $tc = 9$, resulting in 4850 trees used to fit the final model.

Results

GEOGRAPHICAL VARIATION IN TIMBERLINE CHANGE

There is strong evidence that the strength and direction of timberline change has not been independent of geopolitical regions for the 1880–1930 and 1930–2000 periods. Patterns of timberline change were significantly associated with geopolitical region for both time periods (Table 1, Fig. 2), although associations were strongest for the 1880–1930 period ($X^2 = 188.07$, df = 6, $p < 0.001$ for 1880–1930; $X^2 = 15.58$, df = 6, $p = 0.016$ for

TABLE 1

Proportion of timberline length (of 358 km total) to increase in elevation (''rise''), remain at the same elevation (''stable''), or decrease in elevation (''lower'') for four geopolitical regions across two time periods: (a) 1880–1930 and (b) 1930–2000.

Region	Rise	Stable	Lower
(a) 1880–1930			
N. Romania	0.43	0.27	0.30
Ukrainian Carpathians	0.30	0.43	0.28
S. Carpathians	0.41	0.20	0.39
West Carpathians	0.39	0.25	0.36
Totals	**0.37**	**0.32**	**0.32**
(b) 1930–2000			
N. Romania	0.53	0.23	0.23
Ukrainian Carpathians	0.44	0.31	0.25
S. Carpathians	0.52	0.24	0.24
West Carpathians	0.49	0.25	0.26
Totals	**0.49**	**0.27**	**0.25**

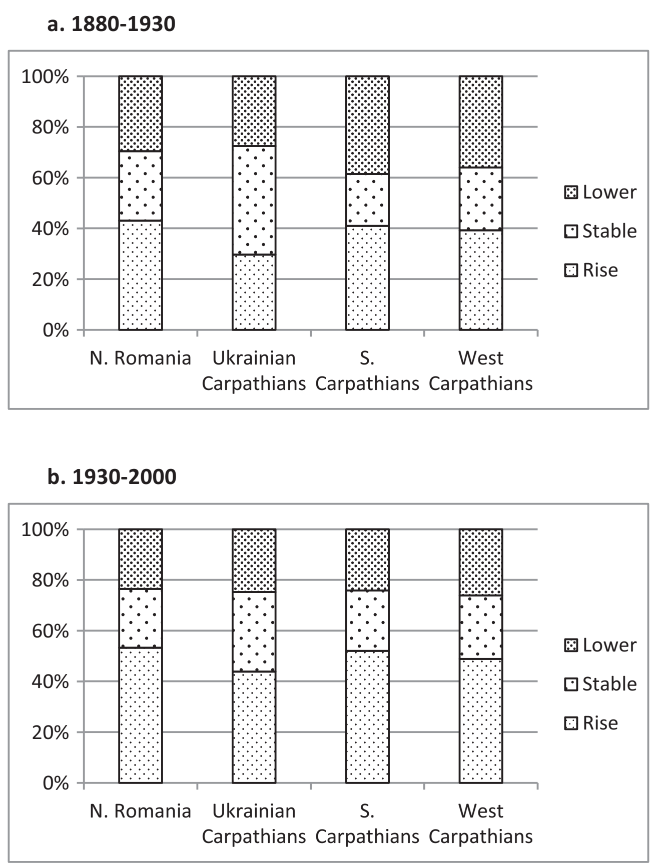

FIGURE 2. Proportion of timberline length to increase in elevation (''rise''), remain at the same elevation (''stable''), or decrease in elevation (''lower'') for four geopolitical regions across two time periods: (a) 1880–1930 and (b) 1930–2000. Actual values given in Table 1.

1930–2000). For both time periods, the Ukrainian Carpathian timberline was the most likely of the four regions to remain stable (i.e. neither elevational decline nor rise was apparent at the 90 m spatial resolution considered). The greatest timberline rises occurred in the North Romanian and South Carpathian regions, whereas the South and West Carpathians showed much timberline lowering in the earlier time period. The 1880–1930 time period showed comparable frequencies of timberline lowering and rising (37% rising to 32% lowering, pooled across regions), with the exception of North Romanian, where timberline rose more than it lowered. In contrast, the 1930–2000 period showed a much greater ratio of timberline rise to timberline lowering (49% rising to 25% lowering).

SPATIAL VARIATION IN THE MAGNITUDE OF TIMBERLINE RISE (1930–2000)

Mean increase in timberline rise (ED) from 1930 to 2000, for all sites that experienced timberline rise, was 56.9 m (95% CI = 53.4–60.3 m), or an elevational increase of nearly 9 m per decade. The most parsimonious boosted regression tree model for the ED timberline rise variable explained 58% of the deviance (pseudo-R^2) in the training data set and 18% of the deviance in cross-validated data, yielding a cross-validation correlation statistic (cv correlation) of 0.42. The most important predictors identified by the BRT analysis (in order of importance) were slope steepness, the timberline elevation in 1930, shrub cover, and topographic curvature (Table 2). Biophysical variables explained 72% of the modeled variance, whereas cultural variables explained 28%. Elevational increase of timberline was greatest where slopes were steepest, particularly where slope steepness was greater than approximately 25° (Fig. 3). Greater rates of timberline rise were also associated with lower elevations, areas with greater shrub cover, more convex surfaces, south-facing slopes, intermediate distances from primary roads, and lower population densities. There was an important interaction effect between population density and shrub cover (Fig. 4). Where population density was high (>0.0015 people km^{-2}), ED was low regardless of shrub cover. However, ED was strongly influenced by shrub cover where population density was low (<0.0015 people km^{-2}) such that timberline rise was much greater for areas of low population density with high shrub cover.

SPATIAL VARIATION IN THE HORIZONTAL DISTANCE OF TIMBERLINE MOVEMENT (1930–2000)

Mean increase in horizontal distance movement (HD) from 1930 to 2000, for all ''sensitive'' sites that experienced timberline advance, was 187.4 m (95% CI = 168.9–205.9 m), or a horizontal advance of 31 m per decade. The most parsimonious boosted regression tree model for the HD timberline movement variable explained 24% of the deviance (pseudo-R^2) in the training data set and 6% of the deviance in cross-validated data, yielding a cross-validation correlation statistic (cv correlation) of 0.24. The most important predictors (in order of importance) were the distance to sheds and timberline elevation in 1930, each contributing more than 25% of the explained variance, with many other variables contributing lesser amounts (5–8%) including population density, deciduous forest cover, coniferous forest cover, and shrub cover (Table 2). Biophysical and cultural variables explained similar proportions of the modeled variance (55% and 45%, respectively). Horizontal migration of timberline was greatest at locations that were at least 20 km from the nearest shed or shepherd's hut, at low elevations (<1100 m a.s.l.), where population densities were low, and the proportion of deciduous forest cover was low (Fig. 5). Two important interaction effects were identified by the BRT analysis (Fig. 6). Shrub cover interacted with population density such that HD was greatest in areas with low population density and shrub cover of at least 70% (Fig. 6, part a). HD was low in areas with low shrub cover except in areas of the lowest population density, where HD had the potential to be higher. At high population densities, HD was greater if shrub density was high. A second important interaction effect involved deciduous forest cover and elevation in 1930 (Fig. 6, part b). Where deciduous forest cover

TABLE 2

Relative importance values of predictors for the elevation difference (ED) and horizontal migration (HD) of timberline between 1930 and 2000, considering only those areas exhibiting timberline rise. Importance values ≥10% are highlighted in bold.

Variable name	Importance for elevation difference (%)	Importance for horizontal migration (%)
Slope steepness	**17.71**	2.99
Elevation	**12.50**	**26.81**
Shrub cover	**10.07**	4.97
Curvature	9.71	3.41
Northness	7.76	3.24
Distance to primary roads	6.73	4.02
Population density	6.42	6.96
Coniferous forest cover	6.16	5.06
Distance to sheds	5.83	**29.63**
Distance to highways	4.95	2.13
Grass (pasture) cover	4.39	2.58
Railroad density	3.56	1.82
Deciduous forest cover	2.45	6.08
Rock cover	1.45	0.10
Residential area density	0.26	0.19
Cover of logged forests	0.06	0.00

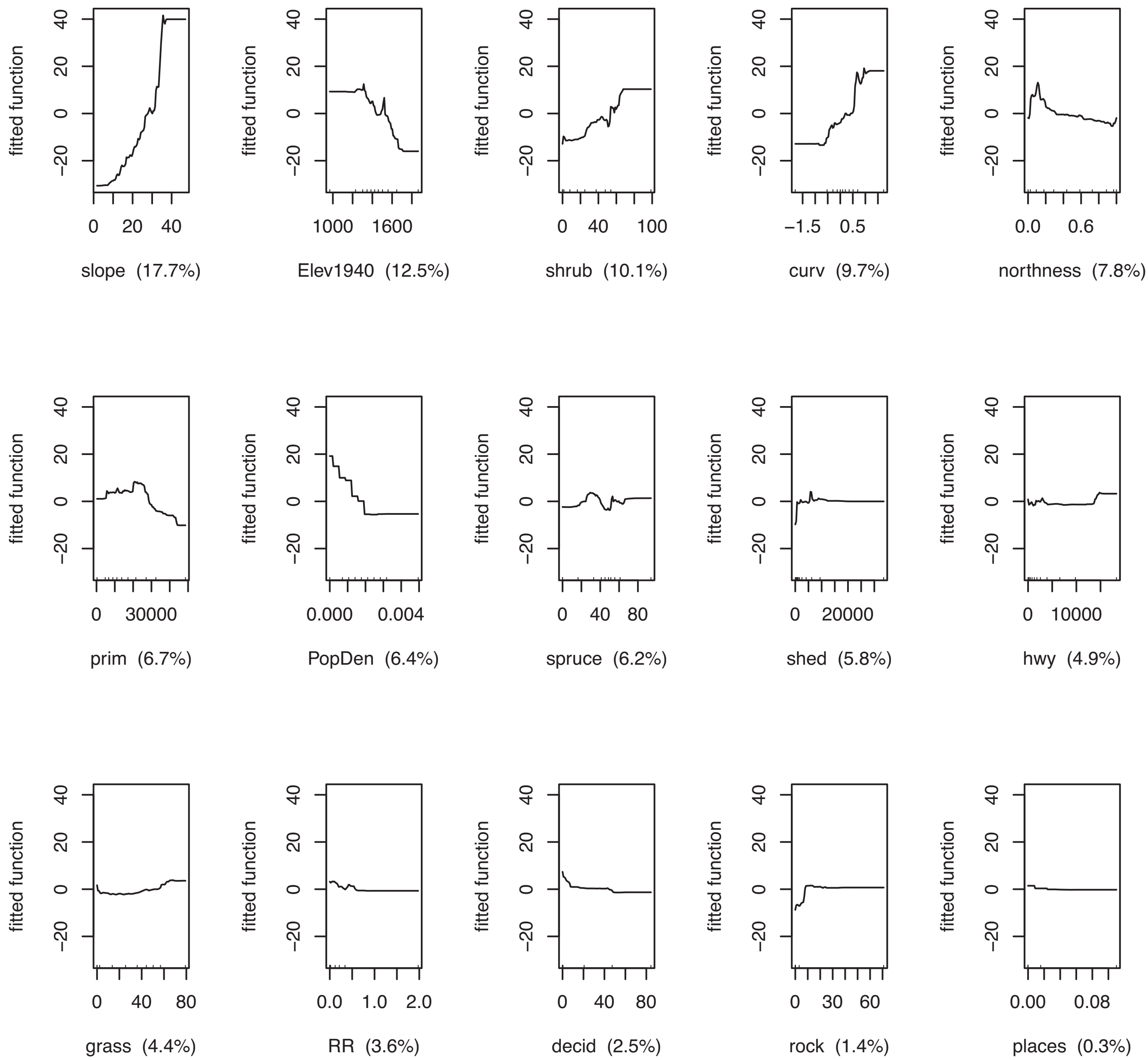

FIGURE 3. Relative influence and partial dependency plots for variables in a boosted regression tree predicting elevational rise of timberline. Partial dependency plots represent the estimated marginal effect of a variable on *y* when all other variables are held at their average. Variable abbreviations: slope = slope steepness (%); Elev1940 = elevation (m) in 1940; shrub = shrub cover (%); curv = topographic curvature index; northness = cosine transformation of slope aspect scaled from 0 (south) to 1 (north); prim = distance to the nearest primary road (km); PopDen = population density (km^{-2}); spruce = coniferous forest cover (%); shed = distance to the nearest shed or shepherd's hut (km); hwy = distance to the nearest highway (km); grass = cover of grass or pasture (%); RR = density of railroads ($km\ km^{-2}$); decid = cover of deciduous forest (%); rock = cover of rocky surfaces (%); places = density of residential areas (km^{-2}).

was high, HD was minimal in all elevations but the lowest. Where deciduous forest cover was low, there was a steady increase in HD with declining elevation.

Discussion

TIMBERLINE CHANGE ACROSS GEOPOLITICAL REGIONS

Our study was novel for analyzing timberline change across political boundaries, using a common methodology for the entirety of a large mountain range occupying 23,260.8 km^2, or 6180 km of timberline length. Across geopolitical regions, timberline rise was more prevalent from 1930 to 2000 than from 1880 to 1930 (Table 1). This observation mirrors similar findings from other studies of smaller areas within the Carpathian ecoregion. In the northern Carpathians, forest cover increase during the 1930–2000 period has been attributed to the direct effects of WWII (or associated post-war resettlement) on dramatically reducing human population, gradual post-war depopulation due to migration to urban

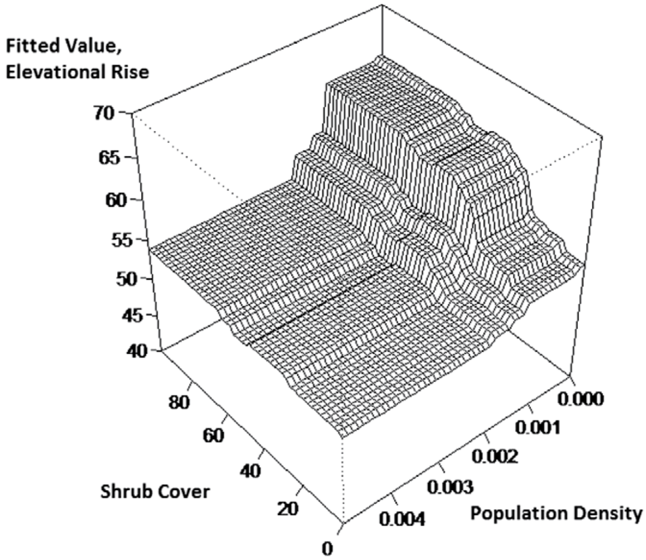

FIGURE 4. Perspective plot showing the fitted interaction effects of shrub cover and population density on the elevational rise of timberline from 1930 to 2000.

centers, and to societal shifts from agricultural to industrial or service-oriented economies (Kozak et al., 2007). In the West Carpathians, grazing pressure has been reduced since the end of WWII due to governmental regulations intended to protect water supply, reduce soil erosion and snow avalanches, and enhance tourism and winter recreation (Plesnik, 1978).

Differences in the strength and direction of timberline change associated with geopolitical region were likely due to differences in political history and land-use changes. For example, a study of forest cover change in an 1843 km^2 area of the West Carpathians, encompassing mostly montane forests in the border region of Poland, Czech Republic, and Slovakia, observed that forest change since the fall of the Iron Curtain has varied with national boundaries in a manner consistent with forest management policy as well as spatial variation in the legacy of Communist-era air pollution (Main-Knorn et al., 2009). Our study found that for the Carpathians as a whole, the magnitude of timberline change was fairly similar across regions except for the greater stability of timberline observed in the Ukrainian region (Table 1). Kozak et al. (2007) also observed less forest cover increase from 1930 to 1990 in the Ukrainian region than elsewhere in the northern Carpathians, consistent with our results. They attributed this relative stability to a lower magnitude of resettlement and subsequent depopulation associated with WWII and its aftermath. The Ukrainian timberline may also have been more stable due to a greater proportion of deciduous, beech-dominated forests (Shandra et al., 2013), as are associated with a lower rate of timberline increase (Figs. 3 and 5).

SPATIAL VARIATION IN TIMBERLINE CHANGE

Neither biophysical variables nor land-use variables alone was sufficient to understand and predict responses of mountain timberlines. As we hypothesized and as other studies have observed (Motta and Nola, 2001; Garbarino et al., 2009; Holtmeier, 2009; Kulakowski et al., 2011), it is the interaction that is important. However, we have shown that for the Carpathian Mountains, the nature of this interaction can be modeled statistically and is weakly predictable.

Our prediction of an inverse relationship between the rate of timberline migration and timberline elevation was supported, after other sources of variation were accounted for, lending support to the hypothesis that timberline migration is influenced by climate once land-use pressures have been removed (Holtmeier and Broll, 2005). Timberline elevational rise was also greater on south-facing slopes, lending further support to a potential temperature mechanism. Following agricultural abandonment, such anthropogenic timberlines may be more sensitive to climate change than natural timberlines lacking a history of intensive land use. Following cessation of grazing, we expect that forest migration at timberline will respond most rapidly at lower elevations where furthest from the true climatic treeline, and least rapidly at higher elevations where tree species are already approaching their thermal limits.

It was unsurprising that steeper slopes were associated with more rapid elevational rise, given that dispersal limitations to migration rate become less important with less horizontal distance to travel. An alternative explanation is that areas of steeper slopes may have been abandoned earlier in the 1930–2000 period due to low suitability for agriculture (Plesnik, 1978; Kozak et al., 2007; Mihai et al., 2007) and so may have experienced timberline migration for a greater number of years. However, the horizontal migration of timberline was only slightly greater on steeper slopes (Fig. 5).

Two competing explanations can be advanced for the association between shrub dominance and more rapid rates of timberline migration (Figs. 3 and 5): (a) direct facilitation, or (b) presence of shrubs may indicate a longer time period of abandonment or more advanced succession. (a) While there have been reports of shrub species facilitating establishment of conifer seedlings by better protection from adverse external factors and injurious climatic influences than grassland communities, commonly known as the nurse shrub phenomenon (Baader, 1995), other studies testify that a dense shrub cover may impair tree establishment by competing with seedlings for light, moisture, and nutrients (i.e. Dullinger et al., 2003). Thus, shrubs may either impede or facilitate tree establishment above the timberline (Holtmeier, 2009). Our results suggest that in the case of the Carpathians timberline, the role of shrubs is a beneficial one for tree establishment. (b) While grazing is still present on mountain pastures, the shrub cover is often burned off to expand grazing area (Sitko and Troll, 2008). Following pasture abandonment, an expansion of shrubs is often observed; hence, a high shrub cover may indicate pasture abandonment, which once again facilitates tree establishment. Thus, shrub cover may be either a cause (facilitation) or a proxy for land abandonment and successional processes. The latter case is suggested by the observed interaction between shrub cover and population density, where high shrub cover is only associated with rapid timberline movement (horizontal or vertical) when population density is low (Figs. 4 and 6). In either case, shrub cover can be a sensitive indicator of the potential for timberline to migrate following land abandonment.

Cultural variables, which were calculated to indicate continued land-use pressure or the likelihood and timing of agricultural abandonment, had greater explanatory power for the HD compo-

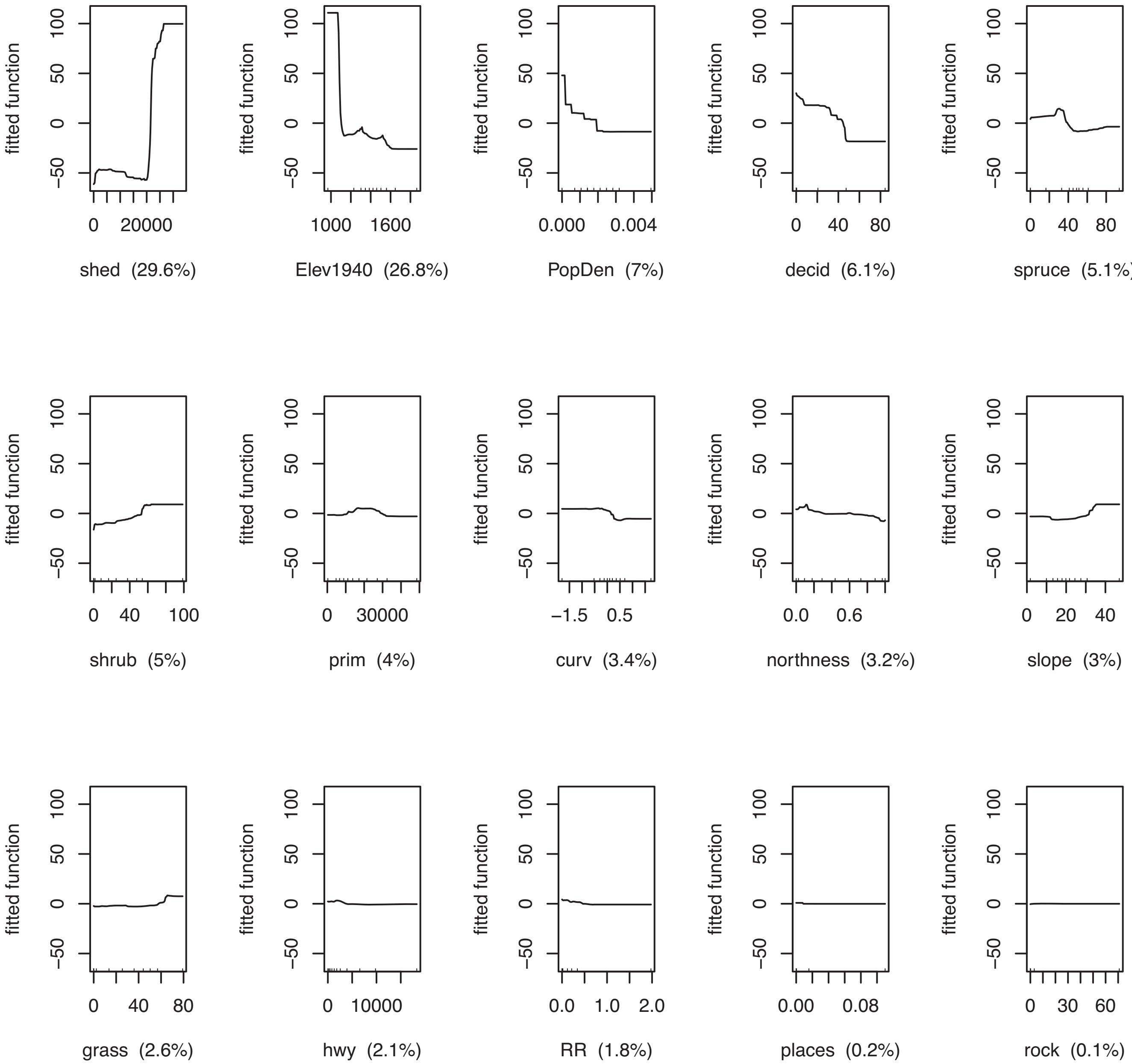

FIGURE 5. Relative influence and partial dependency plots for variables in a boosted regression tree predicting horizontal migration of timberline. Partial dependency plots represent the estimated marginal effect of a variable on *y* when all other variables are held at their average. Variable abbreviations: slope = slope steepness (%); Elev1940 = elevation (m) in 1940; shrub = shrub cover (%); curv = topographic curvature index; northness = cosine transformation of slope aspect scaled from 0 (south) to 1 (north); prim = distance to the nearest primary road (km); PopDen = population density (km^{-2}); spruce = coniferous forest cover (%); shed = distance to the nearest shed or shepherd's hut (km); hwy = distance to the nearest highway (km); grass = cover of grass or pasture (%); RR = density of railroads ($km\ km^{-2}$); decid = cover of deciduous forest (%); rock = cover of rocky surfaces (%); places = density of residential areas (km^{-2}).

nent of timberline movement than for the ED component (47 vs. 32%). Elevational tree migration is expected to be limited more by climate than is horizontal tree migration, since a shift in elevation implies changing temperature and precipitation regimes. The magnitude of timberline migration, considered separately from the elevational component, depends to a large degree on the timing of land-use change allowing trees to establish in former pastures. The ''distance to sheds'' variable proved the most important predictor of HD timberline movement and likely represents a proxy variable for agricultural abandonment. As shown in Sitko and Troll (2008) in a study of the timberline in Chornohora, Ukraine, timberline changes were much smaller around farms, and particularly cattle farms, due to grazing effects on tree establishment and plant community dynamics. While it was impossible for us to distinguish between cattle and sheep farms, it is evident that grazing has been one of the major factors controlling timberline advance. The large importance of this variable in explaining the HD component suggests that when the intensity of grazing decreases, it is possible for

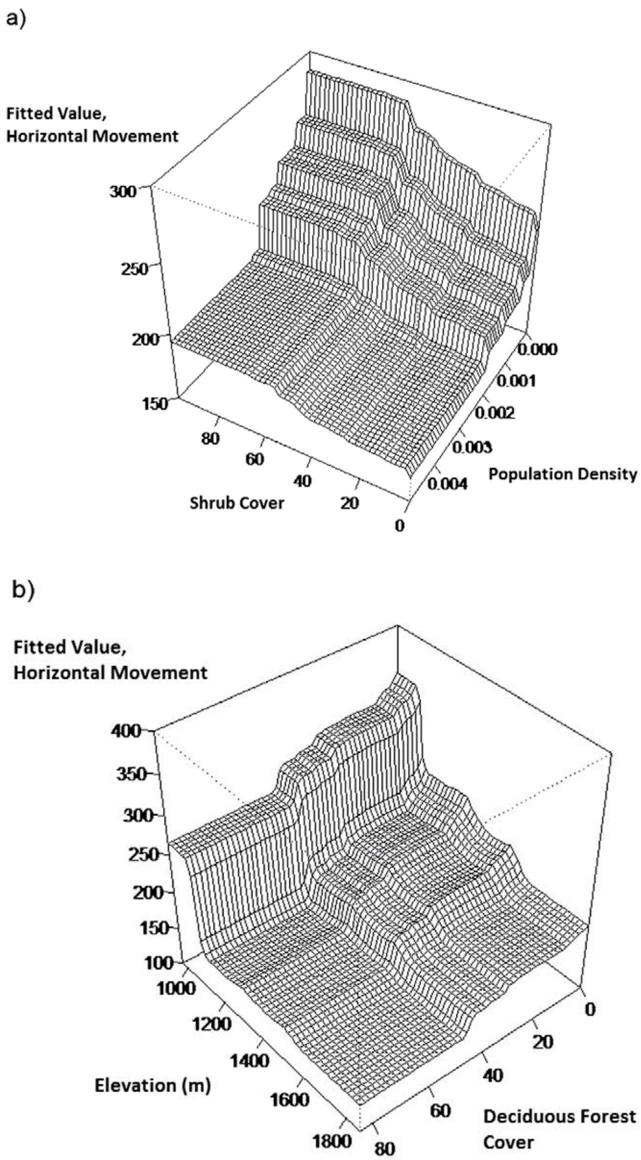

FIGURE 6. Perspective plots showing the fitted interaction effects on the horizontal movement of timberline from 1930 to 2000, for (a) shrub cover and population density; (b) deciduous forest cover and elevation.

tree seedlings to quickly colonize a broad area. Population density estimates, obtained from census data, were also correlated with both HD and ED timberline migration, as was distance from primary roads. Thus, these three variables should prove useful for identifying timberlines of greater sensitivity to climate change. Human population estimates from municipal census data have exhibited strong negative relationships with tree recruitment and timberline expansion in other regions such as the west–Central Alps (Chauchard et al., 2010).

Timberlines dominated by deciduous forest showed relatively limited movement compared to timberlines dominated by coniferous forest, particularly for the horizontal distance measure. The disparity between deciduous and coniferous timberlines is even greater when considering portions of the timberline that did not exhibit any movement over the 1930–2000 time period, which was more likely to be dominated by deciduous beech forest (Shandra et al., 2013). Another study in a relatively localized portion of the Ukrainian Carpathians has observed the same dichotomy, where spruce timberlines have risen considerably while beech timberlines have remained relatively stable (Sitko and Troll, 2008), although others studying the Romanian Carpathians have observed a transition from homogenous, coniferous stands to mixed forest (Mihai et al., 2007). Our results suggest that, at the scale of the entire Carpathian Mountain range but limited to places where timberline rise was observed, the beech forest is less able to respond to the same suitable climate conditions for establishment that lead to a more rapid rise of the coniferous forest following cessation of human land use. This may be due to selective foraging preference of livestock for beech over spruce (Sitko and Troll, 2008). An alternative explanation could be the historical legacy of selective deforestation of spruce forest, leaving the bands of lower-elevation spruce forest intact and creating a novel, anthropogenic beech timberline (Plesnik, 1978). Thus the beech timberline may already be close to its climatic limit, limiting its ability to respond to the combination of agricultural abandonment and favorable climate conditions.

Other explanations for the relative stability of the beech timberline arise from differences in life history traits among dominant tree species in deciduous and coniferous forests of the Carpathians. Based on a simulation modeling study, Bader et al. (2008) observed that strong positive feedback mechanisms among highly shade-tolerant tree species leads to abrupt treeline boundaries and slow rates of treeline advance. Given that *F. sylvatica* is one of the most shade-tolerant European tree species, whereas *P. abies* is only moderately shade tolerant, it is possible that the relative inability of *F. sylvatica* to establish in the open limits its ability to respond rapidly to the combination of land-use cessation and favorable climatic conditions. *F. sylvatica* relies on zoochoric mechanisms for long-distance seed dispersal; seed predation may limit establishment beyond the timberline boundary, particularly during non-mast years (Nilsson and Wästljung, 1987). The timberline boundary of beech forest in the Carpathians is typically quite abrupt (Fig. 7, part a), compared to the more diffuse timberline boundary of spruce forest (Fig. 7, part b).

Conclusions

As reported elsewhere for mountains of the northern hemisphere (e.g. Meshinev et al., 2000; Danby and Hik, 2007), timberlines across the Carpathian range have experienced a net upwards migration since the mid-20th century. However, even during this time period approximately 25% of timberline area has lowered (Table 1), presumably due to continued deforestation associated with logging activity (Dezso et al., 2005; Kuemmerle et al., 2009), agricultural land use and urbanization at lower elevations, and localized natural disturbance events such as snow avalanches (Plesnik, 1978). Cultural influences are critically important for understanding response of mountain forests to global change factors, but in areas where reforestation is already occurring, biophysical influences such as topography, climate, and vegetation play an important role. The rate of timberline response to release from grazing pressure appears to be inversely proportional to elevation. Whether timberline change is considered in its elevational or hori-

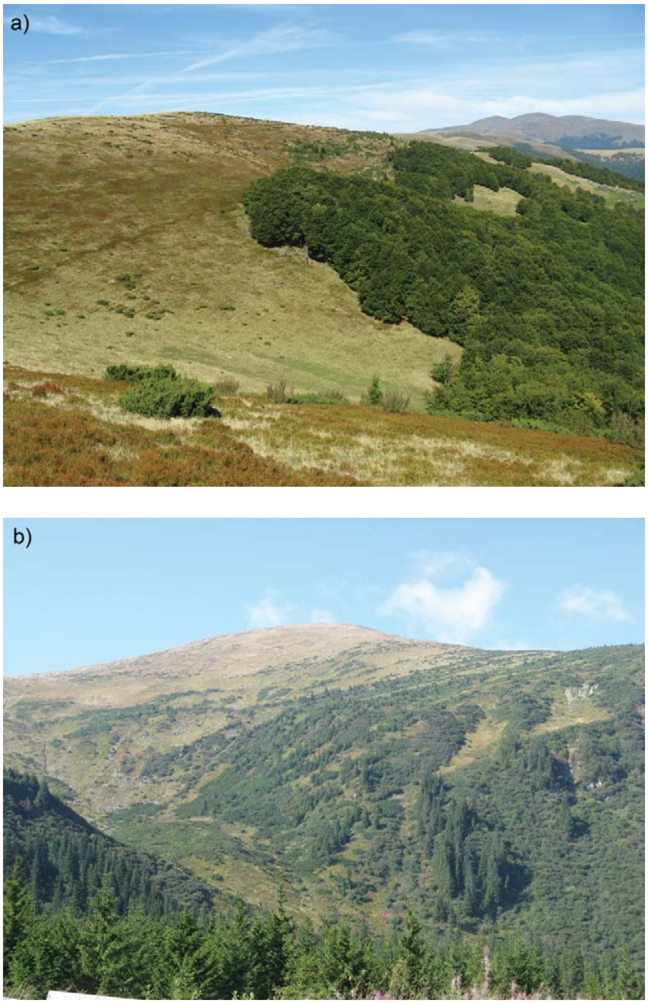

FIGURE 7. Photos from September 2009 showing contrasting timberlines in the Ukrainian Carpathians: (a) abrupt beech (*Fagus sylvatica*) timberline; (b) diffuse spruce (*Picea abies*) and mountain pine (*Pinus mugo*) timberline.

zontal migration component will influence interpretation of amount of change and relative sensitivity to cultural vs. environmental influences. A warming trend, evident in this region since the 1970s, has the potential to accelerate response of timberline position to land-use change, but only for mountain forests where agricultural pressure has been significantly reduced or removed. In such forests, the observed elevational rise of 9 m per decade is comparable to the median rate of 11 m per decade determined from a meta-analysis encompassing studies of numerous plant and animal taxa worldwide (Chen et al., 2011). In Carpathian forests and in other mountain ranges where agricultural abandonment has been prevalent, forest migration in areas with climate warming may increase the contrast in timberline position, and landscape structure of the forest-alpine boundary, among areas with and without intensive land-use.

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