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Pinus mugo Krummholz Dynamics During Concomitant Change in Pastoralism and Climate in the Central Apennines

Li Dai^{1,2*}, Caterina Palombo³, Hein van Gils⁴, David G. Rossiter⁵, Roberto Tognetti^{3,6}, and Geping Luo²

* Corresponding author: daili_helen@163.com

¹ School of Geographic and Environmental Sciences, Guizhou Normal University, No. 116 BaoshanBeiLu, Guiyang, Guizhou 550001, P.R. China

² Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences (CAS), 818 South Beijing Road, Urumqi, 830011, Xinjiang, P. R. China

³ Forestry Labs, Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise, I-86090 Pesche (IS), Italy

⁴ Department of Geography, Geoinformatics and Meteorology, Faculty of Natural & Agricultural Sciences, University of Pretoria, Private Bag X20, Hatfield 0028, Republic of South Africa

⁵ Section of Soil & Crop Sciences, 232 Emerson Hall, Cornell University, Ithaca, NY 14853, USA

⁶ The EFI Project Centre on Mountain Forests (MOUNTFOR), Edmund Mach Foundation, San Michele all'Adige (TN), Italy

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The dynamics of *Pinus mugo* krummholz during concomitant change in pastoral land use and climate in central Italy since the mid-20th century was investigated.

Krummholz dynamics were

detected using sequential aerial photography and fitted to a logistic regression model with elevation, grazing, proximity to beech forest, and proximity to krummholz as explanatory variables. Dendrochronological series were correlated with temperature and precipitation and fitted to a linear model. During this period krummholz doubled in extent and migrated 35–65 m upslope. Expansion was positively associated with

krummholz proximity, residual pastoral grazing, and proximity to beech forest beyond 10 m and negatively associated with elevation and beech forest closer than 10 m. The logistic regression model forecasts krummholz migration by an additional 30 m upslope by 2060. During the 20th century, winter and spring minimum temperatures increased but did not result in increased radial stem growth of *P. mugo*. The combined evidence suggests that krummholz dynamics can be explained by the legacy of summer pastoralism and the dispersal limitations of *P. mugo*, rather than by climate change.

Keywords: Land-use change; pastoralism; climate change; *Pinus mugo*; krummholz; forecast; dendrochronology; Italy.

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Introduction

The dynamics at the alpine treeline modify biodiversity (Stanisci et al 2005), alter landscapes, influence stakeholder benefits (Grace et al 2001), and have significant implications for the carbon cycle (van Gils et al 2008). From the Alps to the Himalayas the prevailing treeline in extra-tropical Eurasia is located below the climatic treeline due to centuries of downslope pasture extension (Ellenberg 1978; Blyakharchuk et al 2007; Miede et al 2007; Fazlur-Rahman 2009; Tattoni et al 2010). Today's anthropogenic treelines include stunted *Pinus mugo* Turra, known as “krummholz” or “crooked wood” (Horvath et al 1974; Palombo et al 2013). Natural alpine treelines are rare in extra-tropical Eurasia (Gehrig-Fasel et al 2007; Dai et al 2013) but widespread on continents without a history of alpine pastoralism.

The contemporary dynamics of anthropogenic treelines is attributed to either abandonment of pastoralism (Dullinger et al 2004; Gehrig-Fasel et al 2007; Chauchard et al 2010; Tattoni et al 2010), climate change (Boden et al 2010; Díaz-Varela et al 2010), or their combination (Motta et al 2006; Palombo et al 2014). An increase in ambient temperature raises the thermal boundary of vegetation growth and induces treeline dynamics (Körner 1998; Harsch et al 2009). Gottfried et al (2012) studied vegetation at the treelines of 60 summits in all major European mountain ranges and concluded that climate change gradually transformed mountain plant communities. Further, land use change, specifically abandonment of farmland and alpine pasture, has led to invasion by woody vegetation (Gehrig-Fasel et al 2007; van Gils et al, 2008; Palombo et al 2014).

Efforts to distinguish between land use and climate-driven dynamics at the treeline appear to be limited to

locations of relatively low elevation (<2500 m asl) and high latitude (>45°) as well as places where abandonment of pastoralism predates 20th-century climate change. In contrast, the *P. mugo* krummholz treeline in the central Apennines is at higher elevation (>2500 m asl) and lower latitude (42° N) – and is situated in the Mediterranean basin where a reduction in summer rainfall and above-average warming is predicted (IPCC 2007) and where abandonment of pastoralism is concomitant with 20th-century climate change (Palombo et al 2013). Treelines above 2500 m asl are common in midlatitudinal (30–45°) Eurasia. The dynamics of anthropogenic treelines have been correlated to climate changes by spatial overlay (Gehrig-Fasel et al 2007; Díaz-Varela et al 2010), regression (Dullinger et al 2004), and circumstantial evidence (Motta et al 2006; Chauchard et al 2010). These studies have extrapolated climate change from meteorological measurements outside the research sites at elevations below the treeline, generally without validation for the study sites. In cases where validation of the extrapolation has been attempted (Dullinger et al 2004), it only covers a fraction of the modeling time span. Moreover, recent research suggests that the pattern of climate change at midlatitudinal high elevations, such as our research site, differs from that at lower elevations (Liu et al 2009; Lu et al 2010). Finally, no previous research provides a spatially explicit forecast of krummholz migration direction and rate.

Remote sensing images, especially from spaceborne sensors, have not been widely used for the treeline studies due to their relatively recent availability (from late 1970s) and the coarse spatial resolution (approximately 80 m) of early imagery. Aerial photographs (APs) are appropriate for historical treeline change detection because of their longer availability (from the early 1950s) and finer spatial resolution (<1 m) (Okeke and Karnieli 2006). A successful method to relate tree growth to local climate at very high spatial and temporal resolutions is dendrochronological analysis (Hoch and Körner 2009); this is especially applicable where the historical climate record is unavailable at high elevations. Treeline change studies using both sequential APs and dendrochronological analysis have seldom been reported in the scientific literature.

Therefore, the aim of this study was to identify, model (second half of the 20th century), and forecast (first half of the 21st century) the dynamics of *P. mugo* krummholz in the central Apennines, with particular focus on the possible impacts of summer pastoralism, climate change, and neighborhood and other environmental predictors. Our research was based on spatiotemporally consistent krummholz and climate change measurements using the dendrochronology of *P. mugo* as an in situ proxy for climate changes. The following hypotheses were tested:

1. *P. mugo* krummholz expansion has been predominantly into abandoned pastures in the beech forest belt below

today's treeline during the second half of the 20th century (H_0), or the krummholz extent below the treeline is stable (H_1). The null hypothesis is suggested by beech forest expansion into montane pastures in the central Apennines (van Gils et al 2008) and in the Alps (Dullinger et al 2004).

2. *P. mugo* krummholz has migrated upward in elevation over the second half of the 20th century (H_0) or is stable (H_1). Upslope migration is plausible given the upslope-migrating beech forest in the central Apennines (van Gils et al 2008). The alternative hypothesis is plausible in view of the stable treeline in the northern Apennines (Holtmeier 2009).
3. *P. mugo* krummholz expansion during the second half of the 20th century can (H_0), or cannot (H_1) be modeled using neighborhood and environmental predictors. The null hypothesis is plausible for neighborhood variables, but not for environmental predictors (Dullinger et al 2004; van Gils et al 2008). If a well-fitting model can be developed, a forecast will be attempted.
4. The high-elevation climate shows a warming trend (H_0) or is stable (H_1) over the 20th century. Global trends and meteorological records from the northern Apennines (Kumar et al 2005) support the null hypothesis. Findings from midlatitudinal high elevations (Liu et al 2009; Lu et al 2010) and from the central Apennines (Izzo et al 2004) suggest that spring and winters may be warmer, but mean annual and summer temperatures are stable (H_1). Any significant climate trends will be used for a forecast.
5. The radial stem growth of *P. mugo* shows that this species is affected by climate warming (H_0) or is stable (H_1) over the 20th century. The null hypothesis (H_0) is supported by findings on the same species from the French Alps and the Apennines (Rolland et al 1998; Palombo et al 2013), the alternative hypothesis (H_1) by dendrochronologies of *Pinus cembra* across the Alps (Carrer et al 2007).

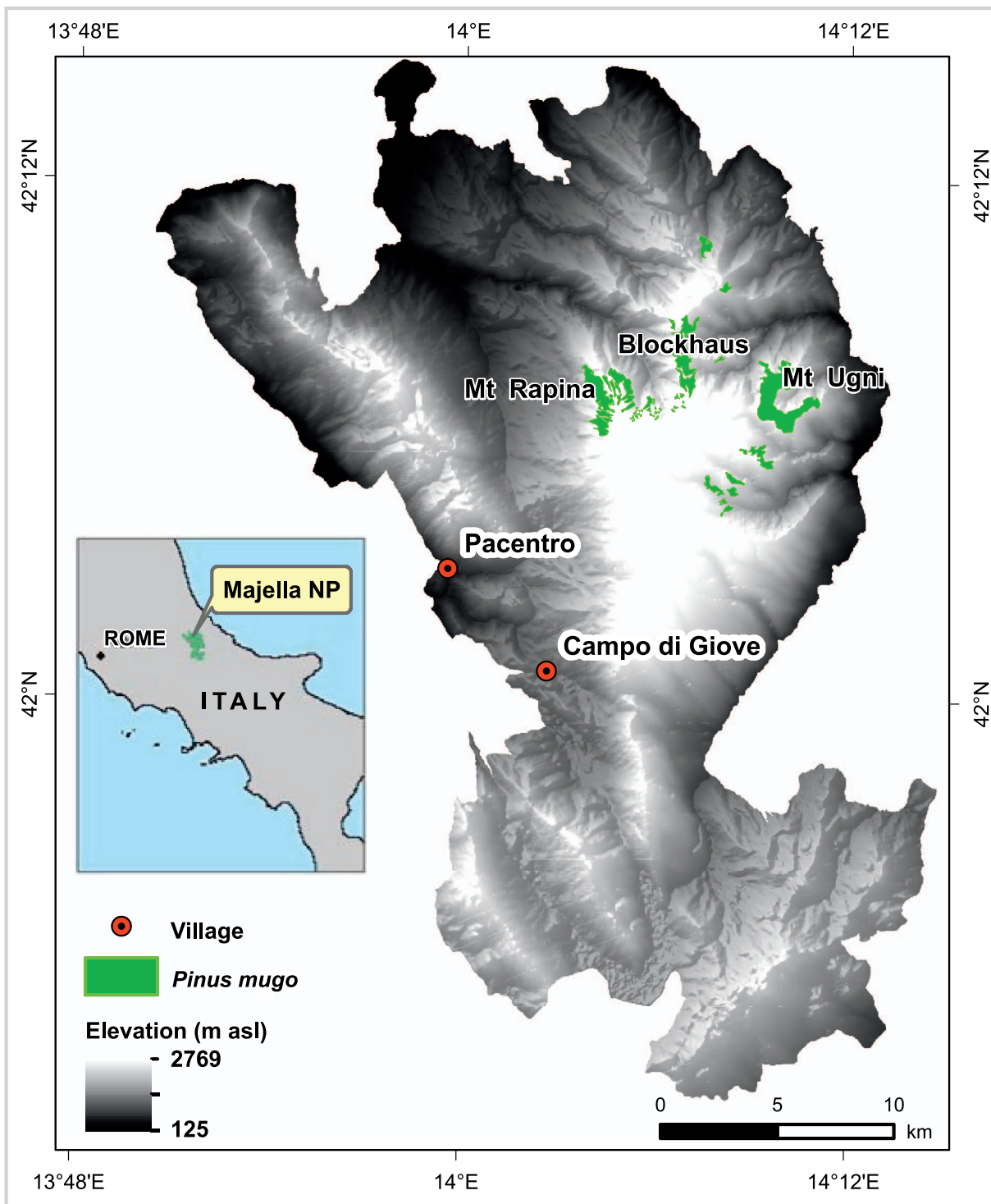
By testing the hypotheses, the relationships among krummholz dynamics, climate change, environmental factors, and anthropic activities were analyzed. Results should be beneficial to policy-makers and local residents designing sustainable development strategies.

Materials and methods

Research area and species

The research area is situated in the humid part of the calcareous Majella massif (reaching 2793 m asl and 32 km from the Adriatic Sea; Figure 1), which has mean annual precipitation of about 1200 mm in Majella National Park (MNP) and 1470 mm at the maritime face of the massif (van Gils et al 2013). Winter precipitation falls as snow above 1400 m asl. The elevational bioclimatic gradient of

FIGURE 1 Location of Majella National Park, with *P. mugo* krummholz distribution (Blasi et al 1999) and the 3 research sites: Mt Rapina (14°4'E / 42°8'N ~ 14°6'E / 42°6'N), Blockhaus (14°6'E / 42°9'N ~ 14°9'E / 42°7'N), and Mt Ugni (14°09'E / 42°07'N). (Map by Li Dai and Hein van Gils)



the Majella massif ranges from arctic-alpine to temperate-montane (uninhabited beech forest belt from 1000 to 1700 m asl) through sub-Mediterranean (broadleaf deciduous oak, hop hornbeam, manna ash forest, and

farmland mosaic) to the Mediterranean biome (olive orchards and evergreen oak forest patches) (van Gils et al 2013). *P. mugo* krummholz covers 14 km² in 3 major patches (Mt Rapina, Blockhaus, and Mt Ugni; Figure 1) at

TABLE 1 Extent and elevation of *P. mugo* krummholz in 1954, expansion during 1954–2007 at the Mt Rapina and Blockhaus sites (Figure 1), and predicted expansion from 2007 to 2060 by the best-fitting model at probability 0.6 at Mt Rapina.

	Extent (km ²)	Elevation (m)
Rapina		
1954	1.25	1399–2573
Expansion	1.65	1427–2608
Site	11.70	1221–2640
Blockhaus		
1954	1.70	1242–2442
Expansion	1.96	1088–2507
Site	17.00	986–2587
Rapina forecasted		
2007	2.90	1399–2608
Expansion	5.10	1244–2638
Site	11.70	1221–2640

elevations of 1221–2640 m (Table 1), that is, below and above the beech forest treeline. Summer pastoralism in the central Apennines dates back millennia (Forni 1998). Pasture has expanded by cutting and burning *P. mugo* (Migliaccio 1966). However, empirical observations have shown that *P. mugo* krummholz is resilient against burning (Leys et al 2014); this is consistent with observations of recuperating krummholz in the Majella massif at the Colle Ingotto (2000–2200m) at the fire scar of the wildfire in 2000 (personal observation by Hein van Gils and Giampiero Ciaschetti; 4 October 2010). Pastoralism declined sharply after World War II and then gradually to the edge of extinction today (Palombo et al 2013; van Gils et al 2013). The herders observed during the field study have abandoned the research area since then (personal communication, Giampiero Ciaschetti; 16 October 2016). The human population has almost halved in the municipalities of the MNP since the 1950s (Comuni-

Italiani 2010). Evidence of abandoned pastoral practices and structures is abundant in the MNP (Micati 2000; van Gils et al 2008; van Gils et al 2010; Manzi 2016).

P. mugo is a prostrate (<5 m) multistemmed, invasive (Kasak et al 2015), woody plant. Its seeds are dispersed by gravity, wind, birds, and seed-caching rodents (Müller-Schneider 1986); layering is common. Seedlings are scarce at close proximity to a seed source (<20 m) and negligible at further distance (>100 m) (Dullinger et al 2004). *P. mugo* krummholz is widespread in the Alps and the Balkans but rare in the Apennines. When present, *P. mugo* dominates the treeline (Dullinger et al 2004; Boratynska et al 2005). It is a pioneer with a fragmented distribution (Ali et al 2006). One of its most geographically isolated locations is the Majella massif (Boratynska et al 2005). *P. mugo* invades avalanche chutes and abandoned subalpine pastureland. This invasion poses a threat to endemic herbaceous species and influences local natural resource management (Dullinger et al 2004; Hoch and Körner 2009).

Change detection

The color 2007 APs served as the reference for orthorectification of the scanned black-and-white 1954 APs (Table 2). Ground truth was obtained in September 2009 by visiting randomly generated points with at least 60-m intervals within a 30-m zone on both sides of hiking tracks passing through the *P. mugo* patches at Mt Rapina ($n=32$) and Blockhaus ($n=79$).

We recorded 4 vegetation cover classes within a plot of 10-m radius at each point: beech forest (>30% canopy cover; tree height >5 m), *P. mugo* krummholz (>30% canopy cover), low vegetation (<30% woody cover; >30% herbaceous cover) and bare ground (<30% vegetation cover). A 5th class, shadow, was distinguished on the 2007 APs. Only 2 classes could be identified on the 1954 APs: forest (beech forest, *P. mugo* krummholz plus shadow) and nonforest (low vegetation plus bare ground).

An automated object-oriented classification computer program (eCognition) was applied to reduce the salt-and-

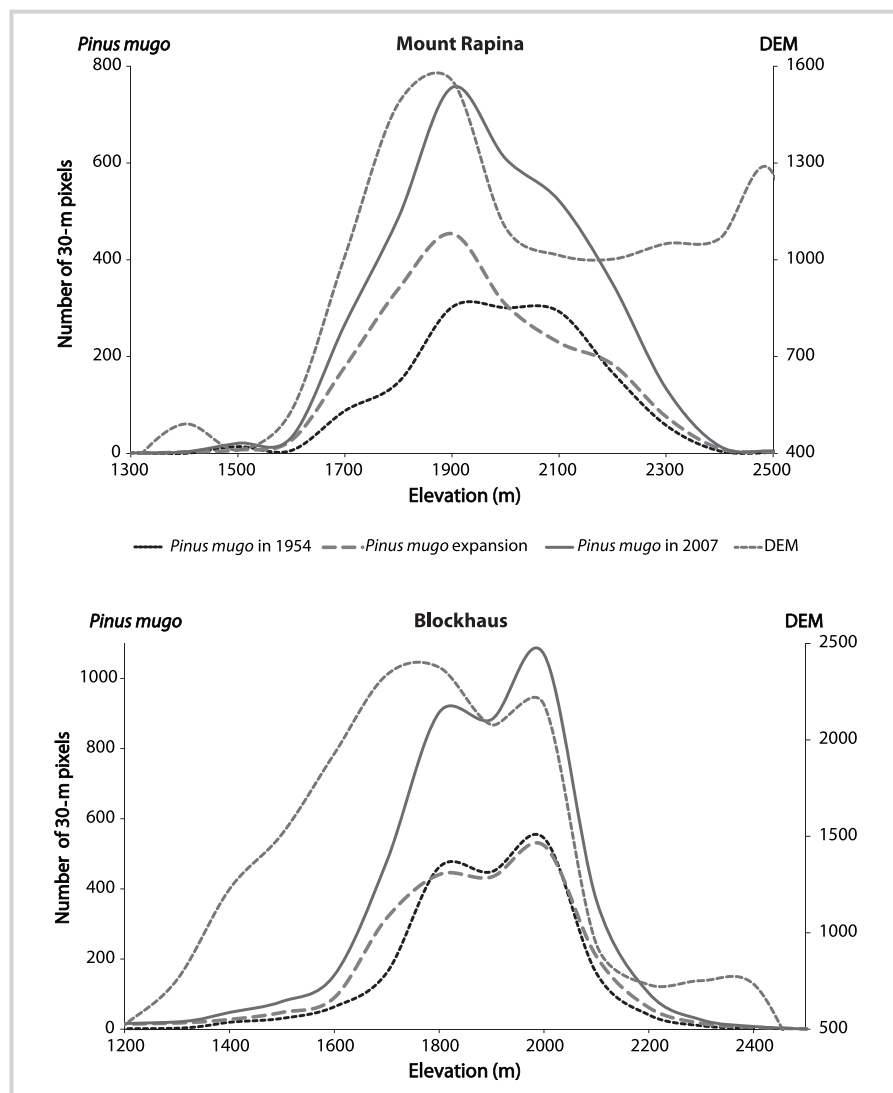
TABLE 2 Input materials for change detection and expansion modeling.

Data	Year	Source	Data type	Scale/Pixel
Aerial photograph	1954	MNP	Analog black and white	1:33,000/0.8 m
	2007	MNP	Digital color	0.5 m
Digital elevation model	2008	ASTER ^{b)}	Raster	30 m
Soil type	1999	MNP	Vector	1:25,000
Residual grazing ^{a)}	1999, 2007	MNP	Vector	1:50,000
Geology	1999	MNP	Vector	1:25,000

^{a)}Source: Simone Angelucci (MNP), 2009: type, number, and location of livestock.

^{b)}Advanced Spaceborne Thermal Emission and Reflection Radiometer.

FIGURE 2 Elevation distribution of *P. mugo* in 1954, in 2007, and expansion from 1954 to 2007 at Mt Rapina and Blockhaus. The dip at 1900–2000 m elevation in the 1954 distribution at Blockhaus is reflected in the 2007 curve and in the expansion curve. (Graphs by Li Dai)



pepper effect (Hay et al 2005) resulting from using high-resolution imagery (Pekkarinen 2002). The object-oriented procedure consisted of multiresolution segmentation and subsequent supervised land cover classification of the segments (Radoux and Defourny 2007).

The ground observations were used for the accuracy assessment of the classified 2007 APs. For the 1954 AP accuracy assessment, cover classes were assigned by visual inspection of the APs in an area with a 10-m radius for around 50 random points per site (Platt and Schoennagel 2009). Agreement between classified APs and ground truth was calculated in R (R-Development-Core-Team 2009). In addition, a weighted Kappa index of agreement was obtained by entering the proportion of each cover class as a weight in the confusion matrix calculation.

Cover changes from 1954 to 2007 were detected using a raster calculator in ArcMap and then intersected with the Digital Elevation Model (DEM) obtaining the upslope krummholz migration. The pixels changed from nonforest (1954) to *P. mugo* krummholz (2007) were assigned as krummholz expansion.

Expansion modeling

Mt Rapina was selected for modeling because of its regular bell-shaped distribution of *P. mugo* krummholz with elevation (Figure 2) and its superior cover-classification accuracies. A logistic regression model was developed using the generalized linear model method in the R environment (Fox 2002), using several relevant predictors (Table 2) according to the hypotheses. The generalized linear model allows a choice of link functions for the

response variable; in this case a binomial response link was chosen. Neighborhoods of 5–100 m for krummholz, and 10–100 m for beech forest in the 1954 APs were tested as predictors, both as ground surface distance and as distance in 2-dimensional (2D) planar projection. In the krummholz expansion area, 2000 random points were generated and intersected with each potential predictor.

The distribution of continuous predictors was tested for symmetry, and those with skewness > 0.5 were log-transformed. The variance inflation factor was calculated to assess colinearity of predictors. The significance of correlations between categorical predictors and krummholz expansion was calculated using the Pearson's chi-square test. After selecting predictors, models with single and multiple predictors were compared for goodness-of-fit using the area under the receiver operating characteristic curve (AUC) and parsimony.

The probability of expansion of krummholz at Mt Rapina for the period 2007–2060 was forecast with the best-fitting model, while substituting the residual grazing map used in modeling (1999) with its 2007 update and the 1954 APs with the 2007 APs. Grazing is the only component of pastoralism for which we have consistent spatiotemporal data at fine resolution; we therefore consider grazing to be a practical proxy of other dimensions of pastoralism, including trampling, debushing (eg van Gils et al 2014), fuelwood harvesting, and purposive burning.

Meteorology and dendrochronology

In the absence of meteorological stations at the research site, records from the only station at alpine elevation in the central Apennines (Campo Imperatore, 2137 m asl; 56 km northwest of Blockhaus) and from 2 nearer stations at lower elevations (Pescocostanzo, 1395 m asl; 26 km south of Blockhaus; Sant'Eufemia a Majella, 870 m asl; 26 km south of Blockhaus) were examined. Pearson's correlations between these 3 stations were calculated for the mean annual and monthly maximum, minimum, and mean temperatures and for monthly total precipitation. To investigate trends, a linear model in R was fit to seasonal temperature and summer precipitation. Seasonal temperature values used were winter (December–January–February), spring (March–April–May) and summer (June–July–August). Summer precipitation was computed as the sum of the July and August values. Because of snowmelt at the treeline in April and May (MNP 2016), moisture limitation for *P. mugo* recruitment seems unlikely in June and therefore we assessed July–August precipitation.

Dendrochronological analysis was conducted at Blockhaus (2000–2100 m) and Mt Ugni (2100–2200 m) in 3 plots (30 × 20 m) at 10-m intervals in each site (Figure 1). The 15–20 *P. mugo* specimens with the largest stem diameter were sampled by increment borer in each plot.

Cores ($n = 122$) were dated by counting rings, and ring widths were measured using LINTAB equipment, a stereomicroscope coupled with the Time Series Analysis Program. Individual raw ring-width chronologies were cross-dated visually and checked statistically using the program COFECHA (Grissino-Mayer 2001). The successfully cross-dated individual raw chronologies ($n = 90$) were averaged to obtain a mean raw chronology per plot. Subsequently, Pearson's correlation was calculated for the mean raw chronologies of the 3 plots within each site.

The raw series were averaged per calendar year to generate a mean raw chronology per site, and Pearson's correlation was calculated for the mean raw chronologies of the 3 plots within each site. Successively the individual raw chronologies were averaged per calendar year to generate a mean raw chronology per site, and Pearson's correlation was calculated for the mean raw chronologies of the 3 plots within each site. Successively, the individual raw chronologies were standardized using ARSTAN (Cook and Holmes 1984) to remove variability due to tree age and nonclimatic site factors.

The variability (interannual trend) linked to climate was preserved by standardization of the raw data into indexed chronologies (mean value = 1.0) using smoothing splines, and then by dividing the ring width measurements by the values obtained from the fitted curve. By standardization, mean standard chronologies per plot were created and successively used for climate-growth analyses. In addition, mean standard chronologies per plot were created and then averaged per calendar year to generate master standard chronologies per site.

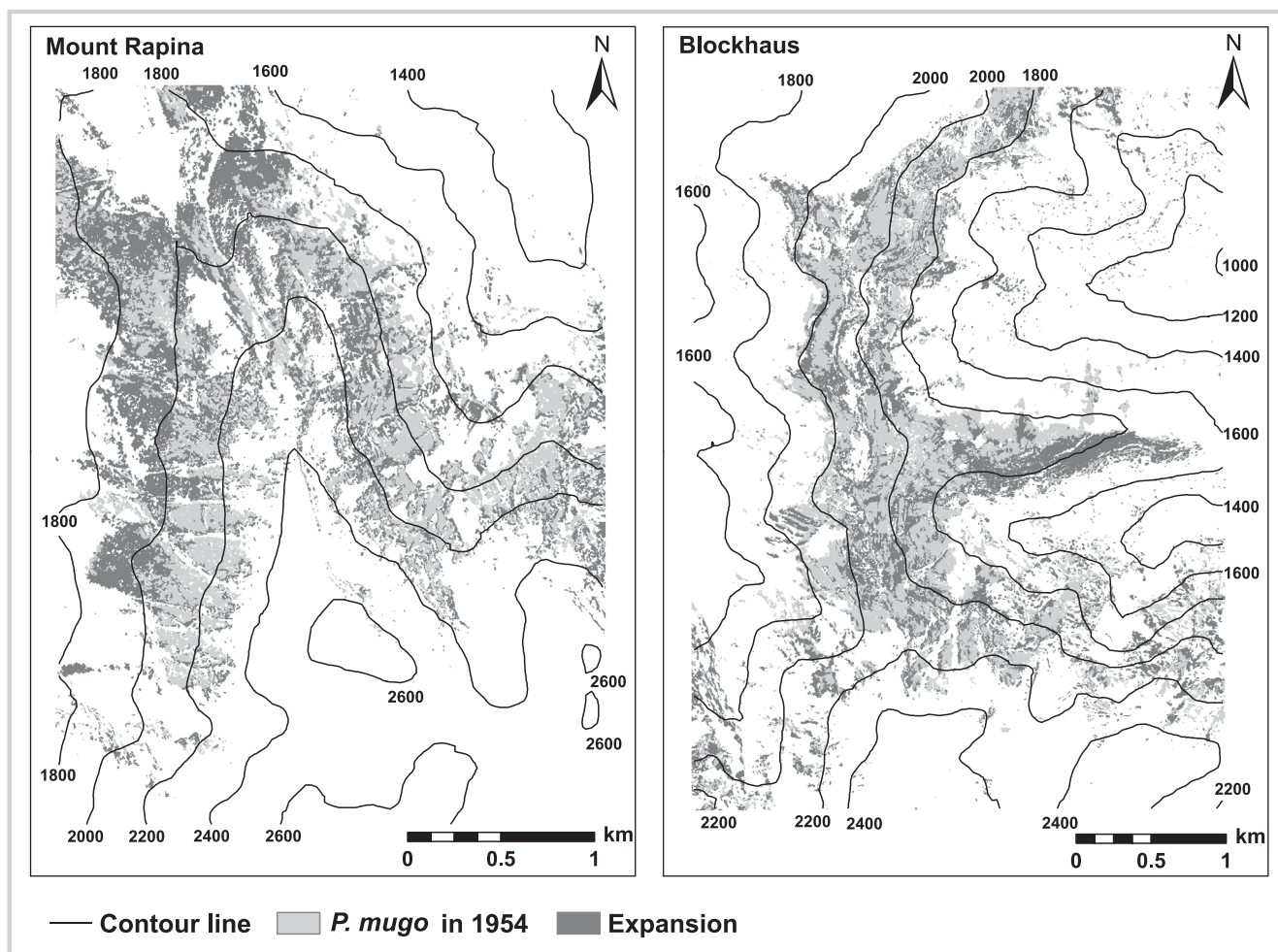
The mean standard chronologies of both sites were correlated with each other and with climate predictors using the linear model in R and examining the model success by the coefficient of determination (adjusted R^2). Forward stepwise linear regression was then applied to the individual predictors with significant relations. The final model was matched with linear modeling assumptions. The relationships between standard dendrochronologies and the climatic data were also assessed by the Pearson's correlation; Student's *t*-test was used to determine its significance.

Results

Change detection and krummholz expansion model

Overall accuracies of the AP classifications were satisfactory (> 0.8) across classes, sites, and years. Krummholz expanded at Mt Rapina and Blockhaus (1.5% year⁻¹ and 1.4% year⁻¹ respectively), more than doubling its extent from 1954 to 2007 (Figure 3), largely within the 1700–2100 m belt (Figures 2; 3; Table 1). At Mt Rapina, the treeline migrated 35 m (2573 to 2608 m) and 65 m at Blockhaus (2442 to 2507 m) (Table 1). The elevation distribution and expansion curves of *P. mugo* krummholz

FIGURE 3 *P. mugo* krummholz expansions from 1954 to 2007 at Mt Rapina and Blockhaus. (Maps by Li Dai)



at Mt Rapina and Blockhaus are bell-shaped with a dip from 1900–2000 m at the latter (Figure 2).

A full model included solar radiation, which was not a significant predictor and thus dropped, while a reduced model was highly significant ($P < 0.005$). All neighborhood variables were associated with *P. mugo* expansion. Combining the best neighborhood predictors in the nested model yielded the proximity to krummholz (planar 2D) and the proximity to beech forest (surface distance) as the better distance predictors (Table 3). The remaining potential predictors showed no collinearity (variance inflation factor < 10). All categorical variables were significantly ($P < 0.005$) associated with *P. mugo* expansion.

A single predictor, proximity to krummholz, well explained *P. mugo* expansion (AUC = 0.82). After stepwise elimination of predictors, the best-fitting and most parsimonious model (AUC = 0.87) showed that the probability of expansion significantly increased with the following conditions (Table 3): proximity to *P. mugo* krummholz, presence of residual grazing in 1999,

decreasing elevation, a negative 10-m neighborhood effect of beech forest, and proximity to beech forest beyond this 10-m neighborhood. At the expansion probabilities of 0.7 and 0.6, the best-fitting model generated twice as many true positives as false positives and forecast that the *P. mugo* treeline will be 26–30 m higher in 2060 than in 2007.

Climate trends and dendrochronologies

The temperature and precipitation from Campo Imperatore, Pescocostanzo, and Sant'Eufemia were correlated significantly ($P < 0.001$). Pescocostanzo was selected for further analysis due to its geographic proximity and relatively complete record. The pre-World War I records were discarded because of apparent instrumentation modification after the war. The spring ($2.87^{\circ}\text{C century}^{-1}$; $R^2 = 0.16$) and winter ($4.38^{\circ}\text{C century}^{-1}$; $R^2 = 0.25$) minima have increased since 1919. Summer minimum temperatures increased ($3.17^{\circ}\text{C century}^{-1}$; $R^2 = 0.16$) and summer maximum temperatures decreased (–

TABLE 3 Logistic regression coefficients for the significant predictors in the best-fitting model.

Predictor	Logistic regression coefficient	Probability (> z)
Intercept	-5.65	0.12
Beyond 10 m beech neighborhood	10.95	2.40×10^{-3} *
Beyond 70 m krummholz neighborhood	4.29	5.31×10^{-4} **
No grazing in 1999	-0.67	1.57×10^{-4} **
Elevation	-8.90×10^{-4}	5.79×10^{-3} *
Log surface distance to beech beyond 10 m beech neighborhood ^{a)}	-0.34	1.34×10^{-5} **
Log planar 2D distance to krummholz within 70 m krummholz neighborhood ^{b)}	-0.30	7.21×10^{-3} *
Log planar 2D distance to krummholz beyond 70 m krummholz neighborhood ^{b)}	-1.32	1.17×10^{-5} **

* $P < 0.01$.** $P < 0.001$.^{a)}Shortened in text to "proximity to beech forest."^{b)}Shortened in text to "proximity to krummholz."

2.69°C century⁻¹; $R^2 = 0.12$). A long-term trend could not be detected in the remaining seasonal temperature values, mean annual temperature, or in summer rainfall. The extrapolated trend in spring minima is not predicted to reach the threshold temperature for growth (6 °C; Hoch and Körner 2009) until 2086 (Figure 4).

The mean raw chronologies per plot at both sites were significantly ($P < 0.01$) correlated (Blockhaus: 0.45–0.81 and Mt Ugni: 0.22–0.62), allowing averaging per site. The

P. mugo radial growths at Blockhaus and Mt Ugni were moderately ($r = 0.58$) and positively correlated for the same years, while showing no temporal pattern over the 20th century. A quarter of the *P. mugo* growth was predicted at both Blockhaus ($R^2 = 0.25$) and Mt. Ugni ($R^2 = 0.22$) from the spring maximum temperature and the summer rain (Figure 5). The warmer the spring or the wetter the summer, the larger the radial growth in the same calendar year.

FIGURE 4 Trend in spring mean minimum temperature from 1928 to 2007 and extrapolation to 2086 (solid red line) with confidence intervals (dashed red lines) and prediction intervals (dotted blue lines). The temperature values (Pescoconstanzo 1395 m) cannot be taken as representative for the krummholz sites above the treeline, only the trend. The actual temperature values may be lower by several degrees. The predicted minimum does not reach the plant-physiological threshold for growth of 6°C during the extrapolation period. The upper 95% interval reaches the threshold in 2011 and the upper 95% confidence interval in 2064. (Graph by David Rossiter)

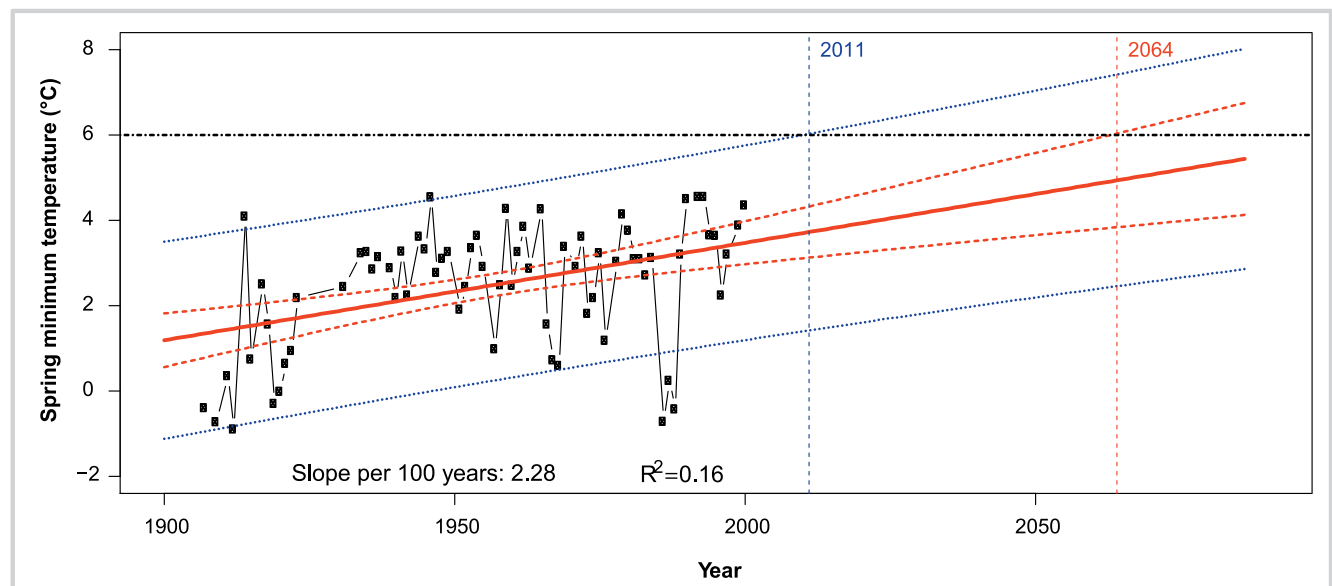
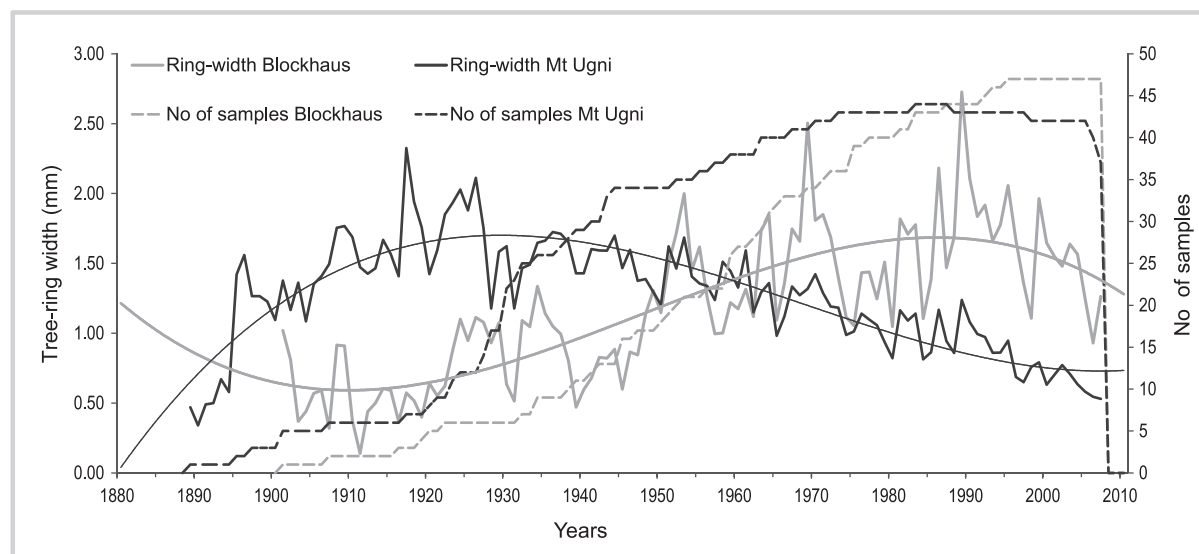


FIGURE 5 Master raw chronologies at Blockhaus (solid grey line) and Mt Ugni (solid black line) with their trend lines; the dotted lines show the number of core samples included in the record. (Graph by Caterina Palombo)



Discussion

Krummholz expansion

The *P. mugo* krummholz expansion rate ($1.4\text{--}1.5\%$ year⁻¹) is similar to the beech forest expansion rate in the montane belt of MNP (1.2% year⁻¹) and forest expansion into abandoned farmland across Europe (van Gils et al 2008). The doubling of the krummholz extent in MNP over half a century corresponds to the statistics from Switzerland for all forests extending to the treeline over a 12-year period (Gehrig-Fasel et al 2007). The upslope migration of *P. mugo* krummholz in the central Apennines ($6\text{--}11\text{ m decade}^{-1}$) concurs with the positive trend detected by Palombo et al (2013) and is close to the krummholz expansion in the Alps (13 m decade^{-1} ; Tattoni et al 2010). However, the range of the upslope treeline migration in the Alps is $25\text{--}50\text{ m decade}^{-1}$ (Gehrig-Fasel et al 2007; Chauchard et al 2010).

The slower expansion of krummholz in the central Apennines may be explained by its higher elevation, given that the latter is a negative expansion predictor (Table 3). The single predictor model (proximity to *P. mugo* krummholz) may explain the expansion by the dispersal limitations of *P. mugo*. Further, the best-fitting multipredictor model (Table 3) suggests environmental limitations for *P. mugo* recruitment.

The positive influence of residual grazing in 1999 on *P. mugo* expansion conforms to findings that moderate livestock impact stimulates expansion of woody plants into pastures (van Gils et al 2008; Luo and Dai 2013), possibly in this case through livestock trampling creating a seedbed (Germino et al 2002) or by preclusion of a litter layer unsuitable as seedbed (Dullinger et al 2004). If we accept grazing as a proxy for pastoralism, associated de-bushing may also play a role (Piussi 1994; van Gils et al 2014).

The absence of *P. mugo* within close (10 m) proximity to beech forest may result from moisture depletion by beech roots (Ellenberg 1978) or the shade effect (Holtmeier 2009). At the same time, *P. mugo* expansion is more probable in the close proximity of beech forest beyond a 10 m beech forest neighborhood. This suggests that beech and *P. mugo* share site preferences. Proximity to *P. mugo* as an expansion predictor of the same species is found in the Alps (Dullinger et al 2004). The number of false (33) versus true (66) positives predicted by the best-fitting model suggests that *P. mugo* is slow to expand over suitable sites.

Our significant neighborhood and distance predictors (Table 3) indicate that the seed dispersal mode may have differential impacts on krummholz expansion. Gravity and wind dispersal may drive expansion at close proximity (<70 m). The weaker predictor “beyond 70 m krummholz neighborhood” may be associated with pine-seed dispersal by birds or seed-caching rodents. Further, both distance and neighborhood values appear beyond the range where layering may contribute to krummholz expansion.

Of the tested expansion predictors, 7 are redundant for the best-fitting model, namely stocking density in residual grazing, geology, terrain type, soil type, incoming solar radiation, slope, and aspect. The range in current stocking density (<1 versus >1 sheep ha⁻¹) seems too low for a differential impact on expansion. The substrate (geology, soil type) seems to be homogeneously shallow and calcareous in the study area. The topoclimate (incoming solar radiation, terrain type, slope, and aspect) and substrate variables were also found to be redundant for predicting beech forest expansion on the Majella massif (van Gils et al 2008). The redundancy of topo-climatic variables makes climate warming an unlikely driver of expansion. Instead, the successful single predictor and multipredictor models are primarily

driven by proximity to a seed source, residual grazing in 1999, and avoidance of close (10 m) proximity to beech forest.

Our forecast of the krummholz expansion supports the claim that the regionally rare *P. mugo* krummholz is in no danger of extinction. However, the arctic-alpine vegetation invaded by the krummholz represents a plant biodiversity hotspot (Stanisci et al 2005; van Gils et al 2012). The forecasted further expansion of krummholz may threaten this botanical biodiversity and dependent fauna diversity (Kasak et al 2015).

Climate trends and dendrochronology

The trend and magnitude of rising minimum winter and spring temperatures found in this research is consistent with findings ($+0.4^{\circ}\text{C decade}^{-1}$) at lower elevations in the Apennines (Izzo et al 2004; Kumar et al 2005). The declining summer maximum temperatures during the 20th century in the research area are similar to those measured elsewhere in the central Apennines and differ from trends in increased maximum temperatures from the northern Apennines. The lower elevation of the meteorological stations in the northern Apennines versus central Apennines (Pescoconstanzo 1395 m) may explain the difference, because at midlatitudes elevation positively associates with rising minimum temperatures in spring and winter (but see Hu et al 2014) as well as with less overall climate warming (Liu et al 2009; Lu et al 2010). The extrapolated trend of rising minimum spring temperatures does not reach the threshold for growth during the 21st century (Figure 4), not even in the beech forest belt at 1395 m. This suggests that the *P. mugo* growing season may not be extended during the period of the forecast.

The local long-term climate trend of the 20th century, higher winter and spring temperature minima, appears not to affect radial growth of *P. mugo*. The reason may be that the higher minima are still below freezing point in winter and well below the threshold for growth even in spring at the much lower elevation of Pescoconstanzo (1395 m). Consequently, the current trend of rising spring temperature minima may not result in increased radial growth in the 21st century (Figure 4). The stable climatic growth conditions for *P. mugo* over the 20th century and our forecast of local climate warming in terms of the plant physiological minimum temperature suggest that upslope

migration of suitable krummholz temperature conditions is unlikely within the period of forecast.

Similar to our findings, the effects of current climate change on the elevational position of krummholz seem minor compared with the effect of land use change in midlatitudinal Eurasia (Palombo 2013; Geanta et al 2014; Schickhoff et al 2015). Moreover, the authors of the latter article conclude that krummholz is relatively insensitive to climate change.

Conclusions

The combination of change detection with sequential APs and dendrochronology provides a spatiotemporally consistent method to distinguish between drivers of krummholz changes above and below the beech forest treeline. The short distance migration in elevation of the *P. mugo* krummholz in the central Apennines is consistent with both climate warming and abandonment of pastoralism. The pattern of krummholz expansion is largely determined by proximity of *P. mugo* as seed source. In the krummholz belt, 20th-century climate change is expressed in higher winter and spring minimum temperatures. Although the dendrochronology of *P. mugo* is shown to be a suitable proxy for the occasional warmer springs or wetter summers, no climatic trend was embedded in radial stem growth of *P. mugo*. The declining maximum summer temperatures, stable summer rainfall, and mean annual temperatures at the research site conform to findings from high-elevation areas at midlatitudes in Eurasia but contrast with findings from the Alps and regional predictions.

The forecasts for both krummholz expansion and the local climate suggest that upslope migration of krummholz will be very modest for the foreseeable future. Only the inward expansion within the krummholz belt into abandoned pasture may be substantial. The combined spatial and temporal evidence suggests that the upslope migration of *P. mugo* krummholz since the mid-20th century can be explained by the legacy of summer pastoralism and the dispersal limitations of *P. mugo*. The regionally rare *P. mugo* krummholz is not threatened by extinction in the Majella massif; however, the endemic-rich arctic-alpine vegetation may be compromised by the inward expansion of krummholz.

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