Common Era treeline fluctuations and their implications for climate reconstructions

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ABSTRACT

Two hundred years after von Humboldt's pioneering work on the upper treeline, and many fundamental studies thereafter, the rate of past elevational changes in one of the most fascinating biogeographic boundaries on our planet remains poorly understood. Here, we distinguish conceptually between realised and potential treeline positions and present an ensemble model approach to simulate mean elevational treeline fluctuations for the past 2000 years. Based on dendrochronological summer temperature records, our simple, though efficient model shows that alpine treelines across the Northern Hemisphere were, on average, about 45-50 m higher after the Roman and medieval warm periods compared to their lowest mean position in the 1760s, which likely reflects the accumulated effects of repeated cold spells during the Little Ice Age. We suggest that the simulated mean differences between realised and potential treeline positions can affect the amplitude and variance of tree ring-based temperature reconstructions. Contrary to common belief, we also argue that the current offset between lower realised and much higher potential treeline positions, which appears unprecedented in the past two millennia, does not account for the yet unexplained 'Divergence Problem' in dendroclimatology, a decoupling between increasing temperature measurements and tree-ring chronologies since the 1970s.

1. Introduction

Marking the potential cold distribution limit of upright tree growth (Körner, 2021a), thermally induced, and conceptually defined, treelines increase in elevation towards the equator. The highest treelines reach almost 5000 m asl in eastern Tibet and the Bolivian Andes (Miehe et al., 2007; Hoch and Körner, 2005), whereas the northernmost treeline approaches sea level at circa 73° North on the Taimyr Peninsula in Siberia (Naurzbaev et al., 2002). Despite fundamental research on the eco-physiological drivers of alpine treeline positions (see Körner, 2012 for a review but note that there are many more studies available), spatial modelling of regional and global treeline sites (Paulsen and Körner, 2014; Bruening et al., 2017; Tran et al., 2017), consideration of possible biochemical and biomechanical factors of upright plant growth at cold extremes (Crivellaro and Büntgen, 2020; Crivellaro et al., 2022), and

low-resolution estimates of Holocene treeline dynamics (LaMarche, 1973; Pisaric et al., 2003; Nicolussi et al., 2005; Heiri et al., 2006; MacDonald et al., 2008; Bruening et al., 2018), there are still substantial gaps in our understanding of the pace and amplitude of past and current treeline fluctuations, and particularly about the implications of such changes for tree ring-based climate reconstructions. Furthermore, there are many treeline studies that do not explicitly define the concept of a temperature-controlled, large-scale boundary of upright tree growth, and that do not distinguish carefully enough between the realised local and regional upper limit of tree growth and the potential global treeline, i.e., the position of (realised) tree growth at highest elevation and the (potential) treeline isotherm (Körner, 2021b). However, it is essential to separate the theoretical from the actual niche edge of upright tree growth (Körner, 2021a), because the realised (locally observed) and potential (thermally constrained at the global scale) cold limits of tree

Fig. 1. Alpine treeline ecotones. (A) Bristlecone pines (*Pinus longaeva*) at circa 3450 m asl (118.3° West and 36.6° North) in the Sierra Nevada, USA (picture by Jiri Dolezal). (B) Qilian junipers (*Juniperus przewalskii*) at circa 3500 m asl (98.8° East and 39.2° North) on the eastern Tibetan Plateau, China (picture by Bao Yang). (C) Siberian pines (*Pinus sibirica*) at circa 2000 m asl (85.5° East and 51.1° North) at Mt. Sarlyk in the Altai, Russia (picture by Alex Kirdyanov).

growth are rarely in equilibrium, and in situ treeline investigations therefore almost never reflect conditions of the treeline isotherm.
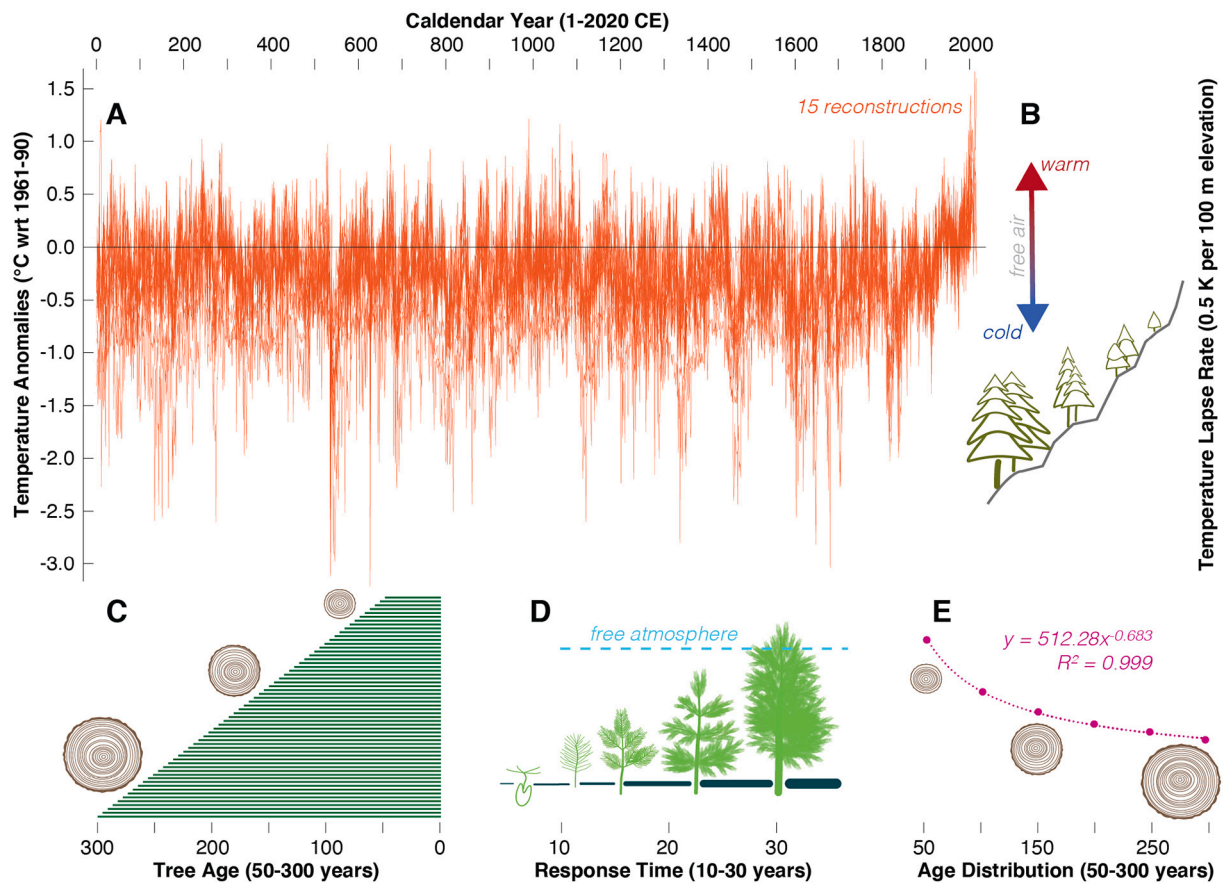
Here, we present the first ensemble model approach for simulating mean elevational changes in both realised and potential treeline positions. Covering the past 2000 years at high temporal resolution and representing alpine treelines across the Northern Hemisphere (Fig. 1), our simple model estimates a mean elevational difference of approximately 45–50 m between the highest and lowest realised treeline positions in the Common Era. We further discuss how past treeline fluctuations can affect the high-frequency variance and long-term

amplitude of tree ring-based temperature reconstructions and call for methodological refinements to overcome associated biases in the paleoclimate record.

2. Materials and methods

We focus on thermally controlled mean elevational changes in alpine treeline positions across the Northern Hemisphere, and we do not engage with locally observed variations in the upper limit of tree growth. We therefore introduce a rather simple model approach that

Fig. 2. Input parameters of the treeline model. (A) Northern Hemisphere summer temperature reconstructions for the Common Era. (B) Free air, mean summer temperature lapse rate of 0.5 K per 100-m elevational difference. (C) Treeline trees of 50–300 years. (D) Between 10 and 30 years of seed germination, sapling formation and upright stem growth. (E) A negative power law to weight tree abundance by age. Our ensemble model approach calculates: 15 temperature records in lapse rates x 2020 years = 30,300 trees (A-B); 30,300 trees × 251 tree ages = 7,605,300 trees (C); 7,605,300 trees × 21 response years = 159,711,300 trees (D-E).

considers an ensemble of 15 tree ring-based large-scale climate re-constructions (Büntgen et al., 2021a). Spanning the past two millennia continuously, these annually resolved and absolutely dated proxy re-cords provide slightly different estimates of summer temperature vari-ability for much of the Northern Hemisphere extra-tropics (Fig. 2A). Considering an annual cycle in elevational lapse rate that ranges from ~0.35 K per 100-m elevational difference in winter to ~0.65 K per 100-m elevational difference in spring (Körner, 2012; Kollas et al., 2014), we apply a mean summer lapse rate of 5.0 K/km to best represent warm season conditions that are most relevant for high-elevation plant growth (Fig. 2B). This linear transformation results in precise estimates of a thermally constrained, potential cold distribution limit of upright tree growth for each year in the past 2000 years, expressed as anomalies relative to the mean Northern Hemisphere treeline isotherm between 1961 and 1990 CE. We assume that treeline ecotones are, on average, composed of 50–300-year-old trees (Fig. 2C), which required approxi-mately 10–30 years to reach sapling stage and become exposed to the free atmosphere rather than growing in their own microclimate (Fig. 2D). We then use a negative power law to account for a higher abundance of younger individuals within the given age distribution of treeline trees (Fig. 2E). In summary, our final ensemble model contains the precise elevational position of circa 160 million trees that have emerged from sheltered boundary conditions of solar ground warming and formed upper treeline ecotones during the past 2000 years.

However, the unvalidated model simulations of mean elevational changes in the realised and potential upper limits of tree growth cannot account for the complex interplay of above- and belowground factors (Hagedorn et al., 2019), non-climatic processes operating at smaller

scales (Holtmeier and Broll, 2005; Körner, 2012), species-specific dif-ferences in growth longevity and climate sensitivity that are most prominent in bristlecone pines (*Pinus aristata*, *balfouriana* and *longaeva*) from the Western USA and Qilian junipers (*Juniperus przewalskii*) on the eastern Tibetan Plateau (Fig. 1) (Salzer et al., 2014; Yang et al., 2014: Bunn et al., 2018; Lyu et al., 2019), as well as spatially heterogeneous temperature variability and geographical differences in lapse rate. Our ensemble model approach therefore provides a simple, temperature dominated mean estimate of past changes in realised and potential treeline positions for the Northern Hemisphere, though fails to explain treeline positions at local to regional scales.

3. Results and discussion

The realised and potential treeline positions for the Northern Hemisphere vary considerably on different frequency domains over the past 2000 years (Fig. 3A). While the potential treeline model is based on 30,300 values and closely follows summer temperatures on interannual to multi-centennial timescales (see Table1 for details), the realised treeline model consists of almost 160 million simulations and reveals a complex trajectory that deviates significantly from Common Era climate variability. Since the Late Antique Little Ice Age (LALIA) in the mid-6th century (Büntgen et al., 2016) leaves a relatively small imprint around 600–650 CE, the largest pre-industrial mismatch between the mean realised and potential treeline positions coincides with the onset of the LALIA in the 530 s CE (Fig. 3B), when the isotherm was on average about 250 m below the treeline trees. Our model simulation further suggests a bias of circa 1.5 K in root-zone temperature measurements of actual
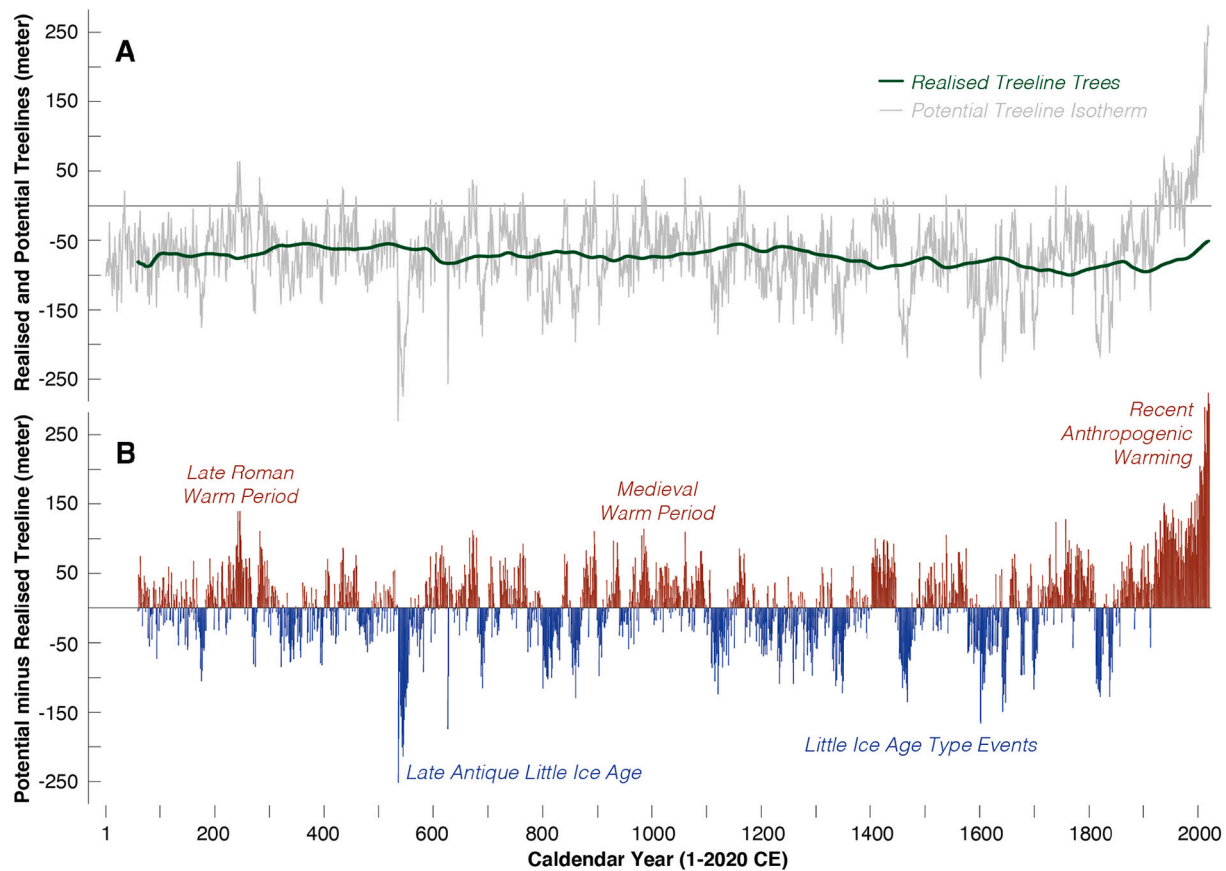
Fig. 3. Simulated treeline fluctuations. (A) Comparison between mean elevational changes of realised and potential treeline positions, i.e., upper tree growth versus thermally-constraint treeline isotherm (see Table 1 for details). (B) Annual differences between the realised and potential treeline positions. All values are expressed as anomalies relative to the potential treeline isotherm between 1961 and 1990 CE.
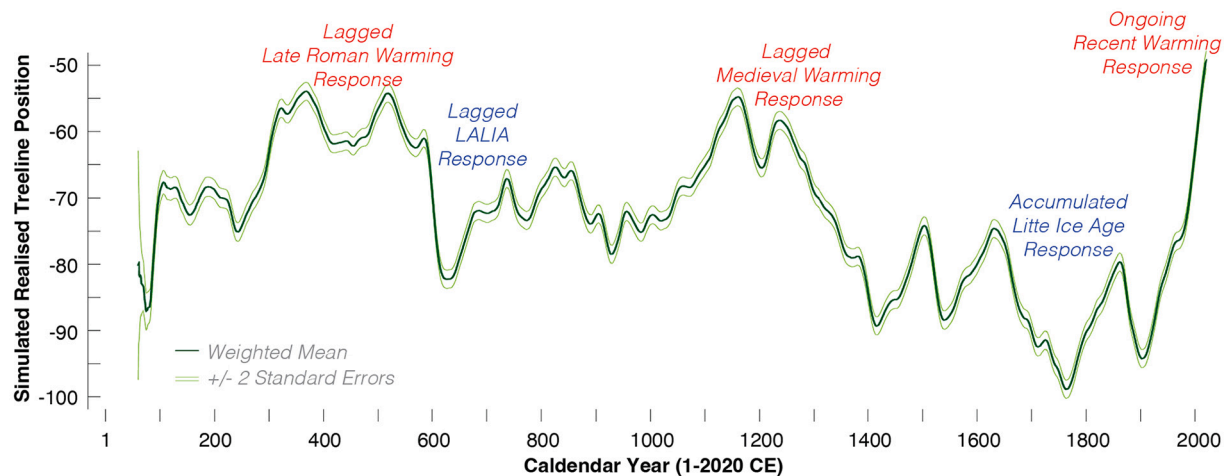

Fig. 4. Simulated treeline positions. Mean elevational changes in the realised position of Northern Hemisphere treeline trees over the past two millennia, expressed as anomalies relative to the potential treeline isotherm between 1961 and 1990 CE.
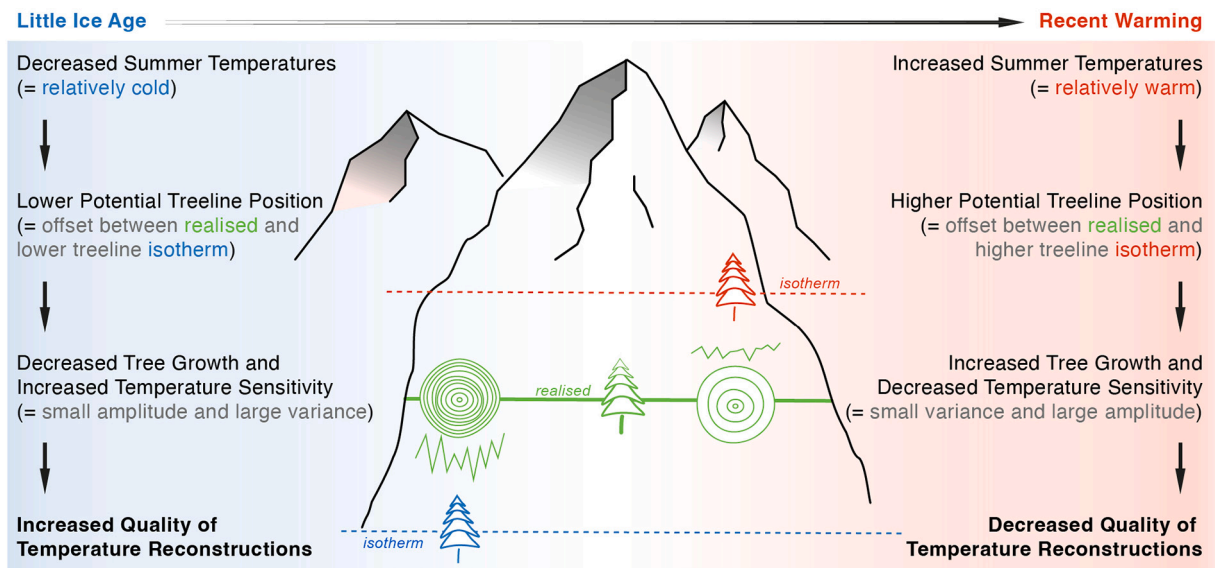
treeline trees (Körner and Paulsen, 2004), which are now growing on average almost 300 m below the potential treeline isotherm. A maximum elevational treeline difference of circa 45–50 m was found during the past two millennia (Fig. 4). The highest realised upper limits of tree growth occurred, on average, around 320–590, 1120–1270 and after 2000 CE, whereas the lowest mean elevation of treeline trees fells in the 1760s (see Table 1 for simulation characteristics). In other words, the highest treeline positions followed the Roman and medieval warm

periods by approximately 80–120 years, whereas the lagged effects of recent warming are not yet fully captured. The lowest treeline position in the second half of the 18th century followed a sequence of Little Ice Age cold spells (Büntgen and Hellmann, 2014) that affected most of the Northern Hemisphere (Büntgen et al., 2020, 2021a). Our high-resolution treeline simulation refines and expands previous estimates from the Polar Ural (Shiyatov, 2003) and the Altai Mountains (Büntgen et al., 2016) (Fig. 5). Moreover, we believe that our simulated treeline

Table 1

Statistical characteristics of the treeline model. Behaviour of our potential and realised treeline models, calculated over the full duration (1–2020 CE), and different periods of time (first and second halves, as well as LALIA, medieval warm period, and LIA). Statistics including the minimum, maximum, mean and median simulation values, as well as their standard deviation and standard error, and their first-order autocorrelation coefficients (from left to right).

	1–2020 CE	1–2020 CE	1–2020 CE	1–2020 CE	1–2020 CE	1–2020 CE	1–2020 CE
	Min	**Max**	**Mean**	**Median**	**STDEV**	**STERR**	**AC1**
Potential Treeline	−308.71	259.80	−67.10	−66.02	54.94	1.22	0.76
Realised Treeline	−98.91	−49.14	−72.83	−72.33	10.83	0.24	1.00
	<1001 CE	**<1001 CE**	**<1001 CE**	**<1001 CE**	**<1001 CE**	**<1001 CE**	**<1001 CE**
	Min	**Max**	**Mean**	**Median**	**STDEV**	**STERR**	**AC1**
Potential Treeline	−308.71	64.58	−67,558.00	−64.08	45.27	1.43	0.65
Realised Treeline	−87.16	−53.92	−68.13	−69.17	7.56	0.25	1.00
	>1000 CE	**>1000 CE**	**>1000 CE**	**>1000 CE**	**>1000 CE**	**>1000 CE**	**>1000 CE**
	Min	**Max**	**Mean**	**Median**	**STDEV**	**STERR**	**AC1**
Potential Treeline	−244.98	259.80	−66.65	−69.25	63.01	1.97	0.81
Realised Treeline	−98.91	−49.14	−77.17	−78.70	11.56	0.36	1.00
	300–600 CE	**300–600 CE**	**300–600 CE**	**300–600 CE**	**300–600 CE**	**300–600 CE**	**300–600 CE**
	Min	**Max**	**Mean**	**Median**	**STDEV**	**STERR**	**AC1**
Potential Treeline	−308.71	24.95	−74.01	−66.68	48.52	2.80	0.70
Realised Treeline	−69.11	−53.92	−58.95	−59.45	3.06	0.18	0.98
	1100–1300 CE	**1100–1300 CE**	**1100–1300 CE**	**1100–1300 CE**	**1100–1300 CE**	**1100–1300 CE**	**1100–1300 CE**
	Min	**Max**	**Mean**	**Median**	**STDEV**	**STERR**	**AC1**
Potential Treeline	−184.16	31.10	−82.05	−83.89	40.08	2.83	0.56
Realised Treeline	−69.10	−54.75	−61.01	−60.82	3.63	0.26	0.98
	1700–1800 CE	**1700–1800 CE**	**1700–1800 CE**	**1700–1800 CE**	**1700–1800 CE**	**1700–1800 CE**	**1700–1800 CE**
	Min	**Max**	**Mean**	**Median**	**STDEV**	**STERR**	**AC1**
Potential Treeline	−185.73	29.76	−65.97	−63.90	40.44	4.03	0.52
Realised Treeline	−98.91	−90.15	−94.24	−93.54	2.72	0.27	0.98

Fig. 5. Conceptual implications of treeline fluctuations. Synthesis of how climate changes affect treeline positions, and in turn the quality of tree ring-based temperature reconstructions. The same factors and processes operate inversely for hydroclimate reconstructions that use data from drought-induced and species-specific lower distribution limits of tree growth.
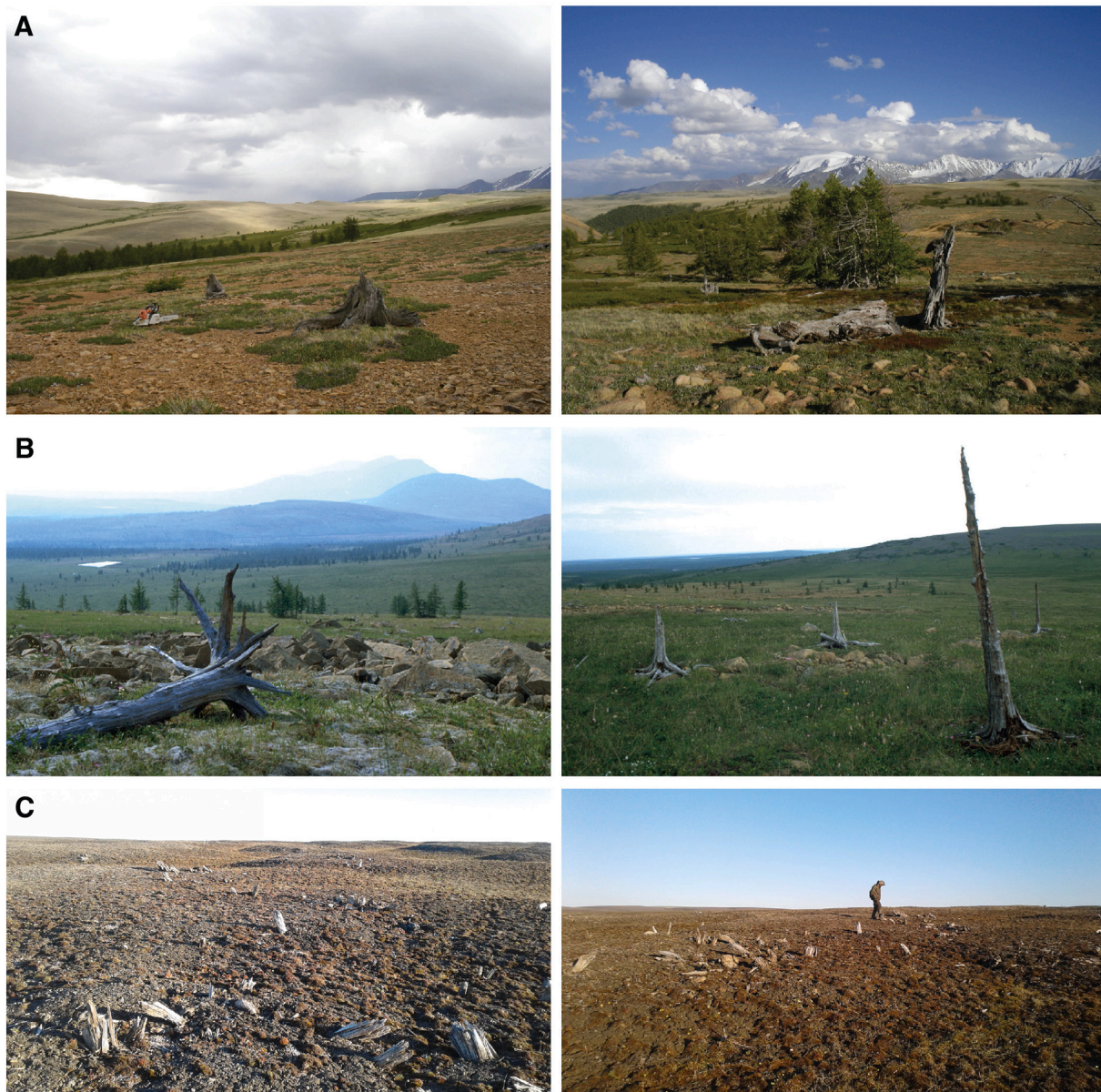
fluctuations will provide an important impetus for comparative studies at the crossroads of paleoclimatology and -ecology, as well as archaeology and history. Interdisciplinary questions of vegetation and land-use/land-cover changes, forest resources and carrying capacity should be addressed independently of past climate conditions. Evidence for this paradigm is particularly strong during the Roman and medieval warm periods, as well as the LALIA and LIA when differences between treeline positions and temperatures were largest, i.e., environmental changes do not have to coincide temporally with climate changes.

We argue that past treeline fluctuations can affect the amplitude and variance (i.e., sensitivity) of tree ring-based temperature reconstructions (Fig. 5). Tree growth below the treeline isotherm, if not affected by drought and other stressors, is usually enhanced and complacent, whereas tree growth above the treeline isotherm would be relatively

suppressed and more sensitive to changes in warm season temperatures. This systematic bias may not only inflate the long-term amplitude between tree-ring reconstructed warmer and colder periods, but also affect the reconstructed interannual variance (i.e., the year-to-year temperature sensitivity). We therefore argue that tree-ring chronologies from elevational or latitudinal treeline sites are likely more accurate summer temperature indicators during cold phases, and possibly overestimate summer temperatures during warm periods (Fig. 5). We assume the opposite is true for tree ring-based hydroclimate reconstructions that may exhibit reduced variance (i.e., sensitivity) and increased amplitude (i.e., growth) during cold and wet periods, respectively.

Furthermore, we suggest that the current offset between lower realised and much higher potential treeline positions, which appears unprecedented in the past two millennia, reduces the growth sensitivity

Fig. 6. Relict treeline evidence. (A) Relict larch (*Larix sibirica*) treeline in the Russian Altai around 2500 m asl at circa 48° North and 88° East, dating into the first half of the CE. (B) Relict larch (*Larix sibirica*) treeline in the Polar Ural around 350 m asl at circa 66° North and 65° East, dating into late medieval times. (C) Relict larch (*Larix sibirica*) treeline on the New Siberian Islands around 40 m asl at circa 75° North and 139° East, dating before circa 50,000 years BP (i.e., radiocarbon (^{14}C) dead). All pictures were kindly provided by Alex Kirdyanov.

of treeline trees to summer temperatures (Fig. 5), but increases stem growth and wood density. Consequently, and contrary to common believe (Camarero et al., 2021; Körner, 2021b), the current mismatch between the realised uppermost forest edge and the much higher potential treeline isotherm fails to explain the putative 'Divergence Problem' in dendroclimatology (Briffa et al., 1998). The 'Divergence Problem' (DP) describes a decoupling between increasing instrumental temperature measurements and tree-ring chronologies since the 1970s that has been reported for some species at some sites (D'Arrigo et al., 2008; Esper and Frank, 2009). The DP, which is not a universal phenomenon (Büntgen et al., 2008; Esper et al., 2010), has recently been associated with the radiative effects of 'Artic Dimming' due to industrial aerosol emissions in the high-northern latitudes (Stine and Huybers, 2014; Kirdyanov et al., 2020; Büntgen et al., 2021b). Though non-relevant to the DP, extreme elevational differences between realised and potential treelines can affect the amplitude and variance of tree ring-based temperature reconstructions (Fig. 5); a bias that has been

broadly ignored by the paleoclimate community.

4. Conclusions

Understanding past treeline dynamics is primarily important because the potential (and conceptual) cold distribution limit of upright tree growth offers a large-scale bioclimatic benchmark for other biogeographic zones on our planet (Fig. 6). Secondly, any elevational offset between the realised local and regional upper limit of tree growth and the potential, thermally driven global treeline position affects the variance and amplitude of tree ring-based temperature (and possibly also hydroclimate) reconstructions, because treeline trees and the treeline isotherm are almost never in equilibrium. Biologists, climatologists, and ecologists investigating the upper limit of tree growth or using data from the corresponding ecotone should therefore consider elevational and climatological offset in their findings and acknowledge that the realised treeline position often results from a complex interplay of various factors

Fig. 7. Dynamic treeline ecotone. An undisturbed alpine treeline ecotone on a north exposed slope in the Swiss Lötschental ~2300 m asl and 46° North and 8° East, where seed germination, sapling formation and the establishment of upright stem growth of larch (*Larix decidua*), pine (*Pinus cembra*), and even spruce (*Picea abies*), recently co-occurs well above the cold distribution limit of the lifeform tree.

and processes (Fig. 1). Biogeographers should continue searching for relict treeline sites (Fig. 6), which may serve as important space-for-time surrogates in paleo-environmental studies. Treeline research may also reflect on the possibility that thermal controls on the lignification of secondary cell walls in the xylem of stems from perennial plants impose biochemical and/or biomechanical constrains for the lifeform tree at its cold distribution limit. Dendrochronologists should overcome the classical lifeform paradigm in plant science and not only expand their studies towards Arctic and alpine shrub, dwarf shrub and herb species, but also towards the assessment of spatiotemporal patterns in seed germination and sapling formation within and above the treeline ecotone to capture rapid responses to recent climate change (Fig. 7). Likewise, paleoclimatologists should explore innovative pathways to detect statistical inconsistencies in their reconstructions, correct artificial variance changes and address pending amplitude issues on inter-annual to multi-centennial timescales. Finally, archaeologists and historians, as well as natural scientists interested in past vegetation and land-use/land-cover changes should distinguish between climate variations and delayed and modified treeline fluctuations.

Author contributions

U·B. conceived the study. U.B., A.P. and A.C. performed the analysis. U.B wrote and revised the manuscript with input from all authors.

Declaration of Competing Interest

The authors declare no competing interests.

Data availability

The ensemble temperature reconstructions and model code are included in the online supplement of this publication.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2022.103979.

References

Briffa, K.R., Schweingruber, F., Jones, P., Osborn, T.J., Shiyatov, S.G., Vaganov, E.A., 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature 391, 678–682.

Bruening, J.M., Tran, T.J., Bunn, A.G., Weiss, S.B., Salzer, M.W., 2017. Fine-scale modeling of bristlecone pine treeline position in the Great Basin, USA. Environ. Res. Lett. 10, 014008.

Bruening, J.M., Bunn, A.G., Salzer, M.W., 2018. A climate-driven tree line position model in the White Mountains of California over the past six millennia. J. Biogeogr. 45, 1067–1076.

Bunn, A.G., Salzer, M.W., Anchukaitis, K.J., Bruening, J.M., Hughes, M.K., 2018. Spatiotemporal variability in the climate growth response of high elevation bristlecone pine in the White Mountains of California. Geophys. Res. Lett. 2018 (28), 13–312.

Büntgen, U., Hellmann, L., 2014. The Little Ice Age in scientific perspective: Cold spells and caveats. J. Interdiscip. Hist. 3, 353–368.

Büntgen, U., Frank, D.C., Wilson, R., Carrer, M., Urbinati, C., Esper, J., 2008. Testing for tree-ring divergence in the European Alps. Glob. Chang. Biol. 14, 2443–2453.

Büntgen, U., et al., 2016. Cooling and societal change during the late Antique Little Ice Age from 536 to around 660 AD. Nat. Geosci. 9, 231–236.

Büntgen, U., Arseneault, D., Boucher, É., Churakova (Sidorova), O.V., Gennaretti, F., Crivellaro, A., Hughes, M.K., Kirdyanov, A., Klippel, L., Krusic, P.J., Linderholm, H. W., Ljungqvist, F.C., Ludescher, J., McCormick, M., Myglan, V.S., Nicolussi, K., Piermattei, A., Oppenheimer, C., Reinig, F., Sigl, M., Vaganov, E.A., Esper, J., 2020. Prominent role of volcanism in Common Era climate variability and human history. Dendrochronologia 64, 125757.

Büntgen, U., et al., 2021a. The influence of decision-making in tree ring-based climate reconstructions. Nat. Commun. 12, 3411.

Büntgen, U., Kirdyanov, A.V., Krusic, P.J., Shishov, V.V., Esper, J., 2021b. Arctic aerosols and the 'Divergence Problem' in dendroclimatology. Dendrochronologia 67, 125837.

Camarero, J.J., et al., 2021. Global fading of the temperature–growth coupling at alpine and polar treelines. Glob. Chang. Biol. 27, 1879–1889.

Crivellaro, A., Büntgen, U., 2020. New evidence of thermally-constraint plant cell wall lignification. Trends Plant Sci. 24, 322–324.

Crivellaro, A., Piermattei, A., Dolezal, J., Dupree, P., Büntgen, U., 2022. Biogeographic implication of temperature-induced plant cell wall lignification. Comm. Biol. 5, 767.

D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the 'Divergence Problem' in northern forests: a review of the tree-ring evidence and possible causes. Glob. Planet. Chang. 60, 289–305.

Esper, J., Frank, D.C., 2009. Divergence pitfalls in tree-ring research. Clim. Chang. 94, 261–266.

Esper, J., Frank, D., Büntgen, U., Verstege, A., Hantemirov, R.M., Kirdyanov, A., 2010. Trends and uncertainties in Siberian indicators of 20th century warming. Glob. Chang. Biol. 16, 386–398.

Hagedorn, F., Gavazov, K., Alexander, J.M., 2019. Above- and belowground linkages shape responses of mountain vegetation to climate change. Science 365, 1119–1123.

Heiri, C., Bugmann, H., Tinner, W., Heiri, O., Lischke, H., 2006. A model-based reconstruction of Holocene treeline dynamics in the Central Swiss Alps. J. Ecol. 94, 206–216.

Hoch, G., Körner, C., 2005. Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. Funct. Ecol. 19, 941–951.

Holtmeier, F.-K., Broll, G., 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Glob. Ecol. Biogeogr. 14, 395–410.

Kirdyanov, A.V., et al., 2020. Ecological and conceptual consequences of Arctic pollution. Ecol. Lett. 23, 1827–1837.

Kollas, C., Randin, C.F., Vitasse, J., Körner, C., 2014. How accurately can minimum temperatures at the cold limits of treespecies be extrapolated from weather station data? Agri. Forest. Meteorol. 184, 257–266.

Körner, C., 2012. Alpine Treelines. Springer.

Körner, C., 2021a. The cold range limit of trees. Trends Ecol. Evol. 36, 979–989.

Körner, C., 2021b. 'Fading of the temperature-growth coupling' in treeline trees reflects a conceptual bias. Glob. Chang. Biol. 27, 3951–3952.

Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31, 713–732.

LaMarche, V.C., 1973. Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. Quat. Res. 3, 632–660.

Lyu, L., Zhang, Q.-B., Pellatt, M.G., Büntgen, U., Li, M.-H., Cherubini, P., 2019. Drought limitation on tree growth at the Northern Hemisphere's highest treeline. Dendrochronologia 53, 40–47.

MacDonald, G.M., Kremenetski, K.V., Beilman, D.W., 2008. Climate change and the northern Russian treeline zone. Phil. Trans. Roy. Soc. B 363, 2283–2299.

Miehe, G., Miehe, S., Vogel, J., Co, S., Duo, L., 2007. Highest treeline in the Northern Hemisphere found in Southern Tibet. Mt. Res. Dev. 27, 169–173.

Naurzbaev, M.M., Vaganov, E.A., Sidorova, O.V., Schweingruber, F.H., 2002. Summer temperatures in eastern Taimyr inferred from a 2427-year late-Holocene tree-ring chronology and earlier floating series. Holocene 12, 727–736.

Nicolussi, K., Kaufmann, M., Patzelt, G., van der Plicht, J., Thurner, A., 2005. Holocene tree-line variability in the Kauner Valley, Central Eastern Alps, indicated by dendrochronological analysis of living trees and subfossil logs. Veg. Hist. Archaeobot. 14, 221–234.

Paulsen, J., Körner, C., 2014. A climate-based model to predict potential treeline position around the globe. Alp. Bot. 124, 1–12.

Pisaric, M.F.J., Holt, C., Szeicz, J.M., Karst, T., Smol, J.P., 2003. Holocene treeline dynamics in the mountains of northeastern British Columbia, Canada, inferred from fossil pollen and stomata. Holocene 13, 161–173.

Salzer, M.W., Larson, E.R., Bunn, A.G., Hughes, M.K., 2014. Changing climate response in near-treeline bristlecone pine with elevation and aspect. Environ. Res. Lett. 4, 114007.

Shiyatov, S.G., 2003. Rates of change in the upper treeline ecotone in the Polar Ural Mountains. PAGES News 11, 8–10.

Stine, A.R., Huybers, P., 2014. Arctic tree rings as recorders of variations in light availability. Nat. Commun. 5, 3836.

Tran, T.J., Bruening, J.M., Bunn, A.G., Salzer, M.W., Weiss, S.B., 2017. Cluster analysis and topoclimate modeling to examine bristlecone pine tree-ring growth signals in the Great Basin, USA. Environ. Res. Lett. 10, 014007.

Yang, B., Qin, C., Wang, J., He, M., Melvin, T.M., Osborn, T.J., Briffa, K.R., 2014. A 3,500-year tree-ring record of annual precipitation on the northeastern Tibetan Plateau. Proc. Natl. Acad. Sci. U. S. A. 111, 2903–2908.