

## Old Juniper Troll stand – The oldest shrub population from Scandinavia

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**Abstract:** Old plant communities are of utmost importance for nature conservation, carbon sequestration, as well as gene pool maintenance. Shrub populations occurring in extreme environments beyond abiotic tree-lines provide diverse ecosystem services and have potential as proxy archives because they often inhabit areas with scarce and short instrumental records. We provide dendrochronological insight into one such population made up of prostrate *Juniperus communis* shrubs in the northern Scandinavian tundra (Norway), growing on a competition-free boulder field. We dated and provided a growth chronology of the oldest living shrub population ( $190 \pm 148$  years) from Scandinavia with the oldest individual being 683 years old. This is a conservative estimate, as shrubs in extreme environments do not form even a single row of cells in some years. The cross-dating issues of poorly growing shrubs do not fully allow to rely on climate sensitivity of the juniper population studied, although the species' potential for dendroclimatological reconstructions is generally considered high, also because the common juniper is an abundant woody species distributed globally. Old populations present an important gene source in plant recruitment, particularly in the context of the present environmental change.

**Keywords:** abiotic tree-line; dendrochronology; *Juniperus communis*; longevity; Sør-Varanger; wood anatomy

Recent nature conservation and climate change mitigation initiatives increasingly focus on research and protection of ancient woodlands and primary forests, as ecologists better understand and recognise their multiple and unique environmental benefits

(Pimm et al. 2018; Di Marco et al. 2019), including their key role as carbon sinks (Luyssaert et al. 2008; Keith et al. 2022). Ecosystems with the presence of old individuals promote – among other ecosystem services – further carbon storage because of their

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long residence times (Kangas, Ollikainen 2022). It is, therefore, essential to investigate and preserve old populations (Keith et al. 2022). Nevertheless, not only trees (Körner 2017) but also shrubs can grow for centuries (Lehejček et al. 2017). The dendrochronological potential of tundra shrubs received broader attention relatively recently due to more advanced methods of their analysis (Kolischuk 1990). Ever since, our knowledge of tundra shrub-dominated ecosystems has grown decently (see e.g. Woodcock, Bradley 1994; Schmidt et al. 2006; Buchwal et al. 2013; Myers-Smith et al. 2015; Wilmking et al. 2018; Lehejček et al. 2023). Those and other studies portray shrub-dominated ecosystems as one of the most heavily affected by current climate change because they are predominantly situated in climatically extreme regions beyond latitudinal and elevational tree lines. Both tundra and semi-arid shrub-dominated communities are facing historically unprecedented changes in climate conditions (Tumajer et al. 2021). Warmer and drier conditions are forecast to put increasing pressure on trees in dry biomes (Bennett et al. 2015). This pressure may then lead to trees being replaced by shrubs (Camarero, Ortega-Martínez 2019). Conversely, tundra shrubs may respond to rising temperatures by increased growth rates and establishment (Li et al. 2016) while being simultaneously suppressed by boreal forests on the other side of the biome gradient. Old shrub communities will therefore likely serve as important genetic reservoirs for shrub expansion towards the new limits (Myers-Smith et al. 2011). Such sites are often located beyond abiotic tree lines under extreme microhabitat conditions, where logging or fire are not likely and the effect of competition or herbivory is limited (Larson et al. 1999).

Here, we provide insight into such an ecosystem by analysing growth patterns and examining the age of old juniper (*Juniperus communis*) shrubs growing on a boulder field in northeast Norway. *Juniperus communis* is the most widely distributed woody plant around the globe, exhibiting unique growth plasticity (Tumajer et al. 2021) and climate sensitivity (Lehejček et al. 2017). Its territory spans all continents of the Northern Hemisphere and most of its biomes (Adams 2008). It is an evergreen, long-lived shrub that often colonises extreme sites (Thomas et al. 2007). The species has strong dendroenvironmental potential (Pellizzari et al. 2014) and its growth parameters have already been successfully used to reconstruct continental ice sheet melt (Buras et al. 2017) or a snowpack duration (Carrer et al. 2023).

To provide the above-mentioned insight, we applied dendrochronological and wood anatomy techniques. We also examine the responsiveness of junipers to the climate by relating ring width measurements to mean temperature and precipitation data.

## MATERIAL AND METHODS

The area of interest is characterised by one of the oldest rock formations in Scandinavia, which originated in the Palaeoproterozoic era. It consists mainly of pink and yellowish-grey arkoses and conglomerates with interbedded greenish-grey sandstones and mudstones (Siedlecki 1980). This region is influenced by the Northern Atlantic Current, which reaches the Barents Sea. The vicinity of the ocean provides a relatively mild climate with a mean annual precipitation total of 561 mm, a mean annual temperature of 0.5 °C and a mean summer (JJA) temperature of 11.0 °C (NMI 2023). Throughout the last century, the study site has been exposed to heavy industrial pollution from a nearby nickel–copper smelter in Nikel (Никель), Russia (Bjerke et al. 2006; Myking et al. 2009).

For this study, we sampled 41 individuals of *J. communis* L., *Cupressaceae* (Figure 1). The sampling site was a large boulder field on a slope by the bank of Gardsjøen Lake, close to the Russian border and the settlement of Grense Jakobselv in the municipality of Sør-Varanger (Troms og Finnmark county in Norway; 69°42'36"N, 30°51'00"E). Boulder fields are characterised by extreme drainage and consist of very dry stands interspersed with moist or wet microhabitats in enclosed pockets and depressions. We designed the sampling to obtain a representative population signal for the site, so we did not select individuals based on their size or other external features. To capture the full variety of plant ages and various sizes, we established a grid, within which we sampled the closest individuals to the grid intersection points. The junipers sampled were of the multi-stemmed prostrate growth form (up to 0.5 m in height), often with twisted or eccentric growth due to harsh climate conditions and occasional disturbance from rockfall. We took basal stem discs (at root collars if accessible) using a hand-saw from each plant to maximise the number of rings and obtain the oldest parts of the plant stems (Schweingruber et al. 2013). All shrubs inhabited an elevation range of 150–180 m a.s.l.

Ring-parameter measurements were taken along the longest axis of stem discs because it is the

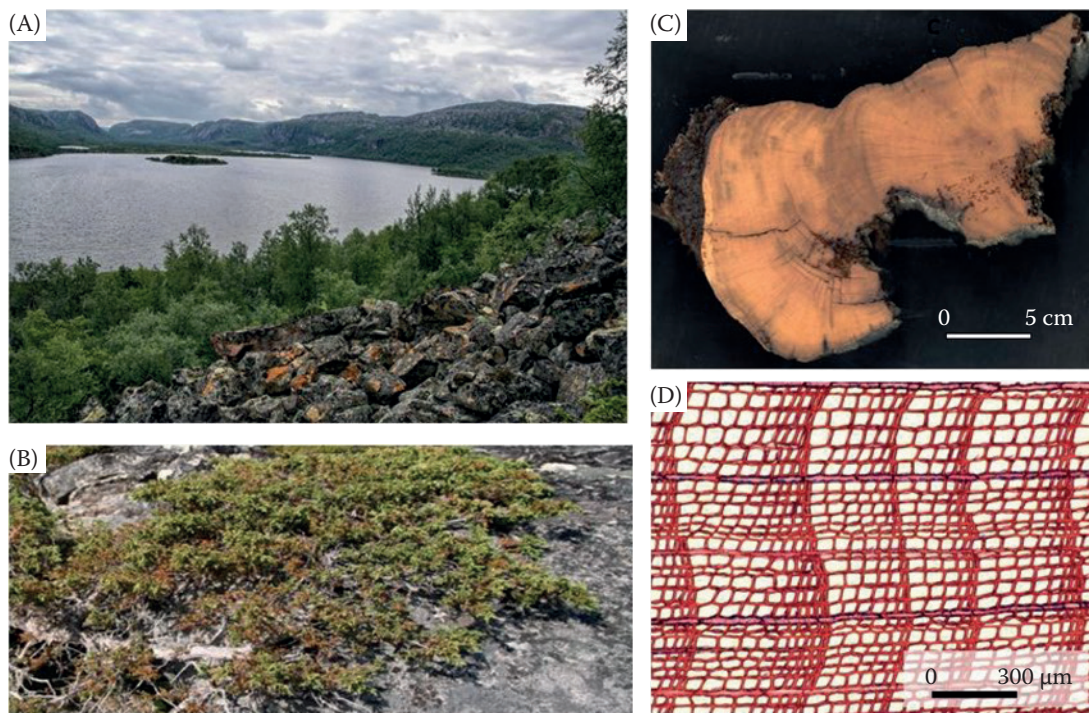


Figure 1. (A) Boulder field hosting a juniper population on a slope by the bank of the Gardsjøen Lake; (B) common juniper on a boulder with its typical prostrate form; (C) stem disc of the oldest individual harvested close to the root collar showing irregular and eccentric growth; (D) microscopic image of a 15 µm thick microtome slice enabling precise annual ring determination, period 1645–1648

least likely to intersect missing or wedging rings. It is therefore the most reliable parameter for subsequent measurements (Schweingruber et al. 2013). The stem discs were hand-sawed in a way so as to obtain a piece of wood with the surface perpendicular to the tracheids and containing the longest axis of the respective stem disc. A solution of corn starch and water was then applied to this surface to stabilise the cell walls and prevent the distortion of the cellular structure (Schneider, Gärtner 2013). The 10–20 µm thick thin-sections were later obtained using a sliding laboratory microtome. Sodium hypochlorite was used as a bleaching agent prior to cleaning the thin-sections with water and double-staining for 5 min in a 1:1 solution of Safranin and Astrablue (the solution used according to Schweingruber et al. 2013), and then washed again. Increasing ethanol concentrations were used (70%, 90%, and 98%, respectively) to dehydrate the samples. Xylene was then applied to eliminate any remaining water in the samples. Finally, the samples were preserved in Canada balsam, embedded under a cover glass (Schweingruber et al. 2008) and dried for at least 12 h at 60 °C.

Images of microsections were taken using a digital camera (EOS 650D; Canon, Japan) connected

to a microscope (BX41; Olympus, Japan) under 100× magnification, and photos were analysed using WinCell Pro 2011 software (Regent Instruments WinRHIZO Pro; 2011). We measured mean ring width along the longest axis of all individuals by manual path analysis using WinCell software. To determine the minimum plant age (Schweingruber et al. 1990), we cross-dated the ring widths in PAST4 (Version 4.2, 2007) and inspected them visually to detect possible missing rings.

Individual tree-ring series were detrended by a 50-year-long spline with a 50% frequency cut-off as a function predicting radial growth. The resulting ring-width indices (RWI) were calculated as ratios between modelled and observed growth (Cook, Peters 1981). Finally, a master chronology was calculated using Tukey's biweight robust mean (R package dplR 1.7.4; Bunn 2019).

We have determined the mean and standard deviation for age, diameter, and increase per year. Using the function 'rwi.stats' (R package dplR 1.7.4; Bunn 2019), we calculated the expressed population signal (*EPS*), the mean inter-series correlation (*Rbar*), and the signal-to-noise ratio in moving 30-year long windows with a 15-year overlap. Ad-





lenge not comparable with any of our previous work (Lehejček et al. 2017; Tumajer et al. 2021). In total, we added 62 missing rings. The age distribution of shrubs in the population is presented in Figure 2C, with their mean age being  $190 \pm 148$  years. This represents the mean annual-ring width of  $0.037 \pm 0.013 \text{ mm}\cdot\text{yr}^{-1}$ . The mean sensitivity was 0.32, the signal-to-noise ratio was 2.83, the  $Rbar$  was 0.06, the  $EPS$  was 0.14 (Figure 2B), the mean first order of autocorrelation was  $0.73 \pm 0.08$ , and the mean correlation of the individual series with the chronology was  $0.22 \pm 0.10$ .

The linear model explaining  $Rbar$  by age classes (negative effect) was highly significant ( $P = 0.01$ ) with 83% explained variability (Figure 3), while the effect of the number of discs was positive ( $R^2 = 0.56$ ), however insignificant.

The climate-growth correlations of tree-ring chronology were in general quite weak and insignificant. The only statistically significant responses were the positive influence of precipitation in January and the positive effect of temperatures in May and July. The highest correlation (0.32) was with mean current summer temperatures (May–August; Figure 4).

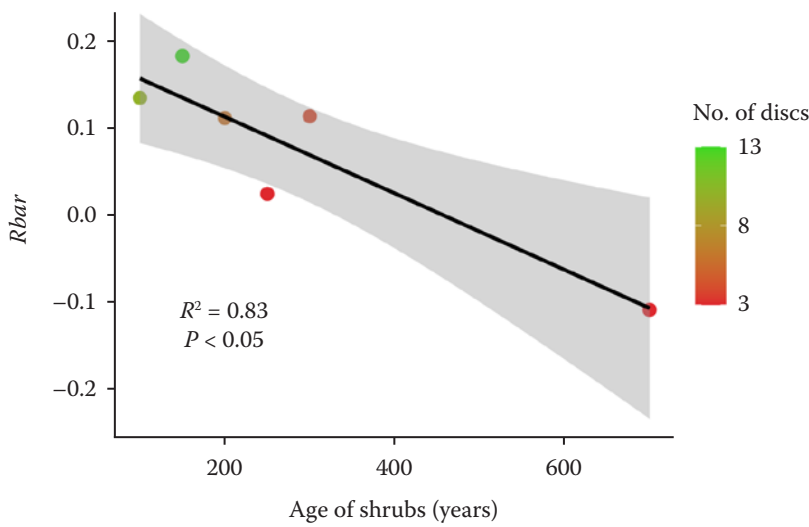


Figure 3. Relationship of age classes and mean inter-series correlation ( $Rbar$ )

Colours from red to green – number of cores in a given age class from low to high, respectively; black line and shaded area – linear trend and confidence interval (95%) between  $Rbar$  and age class

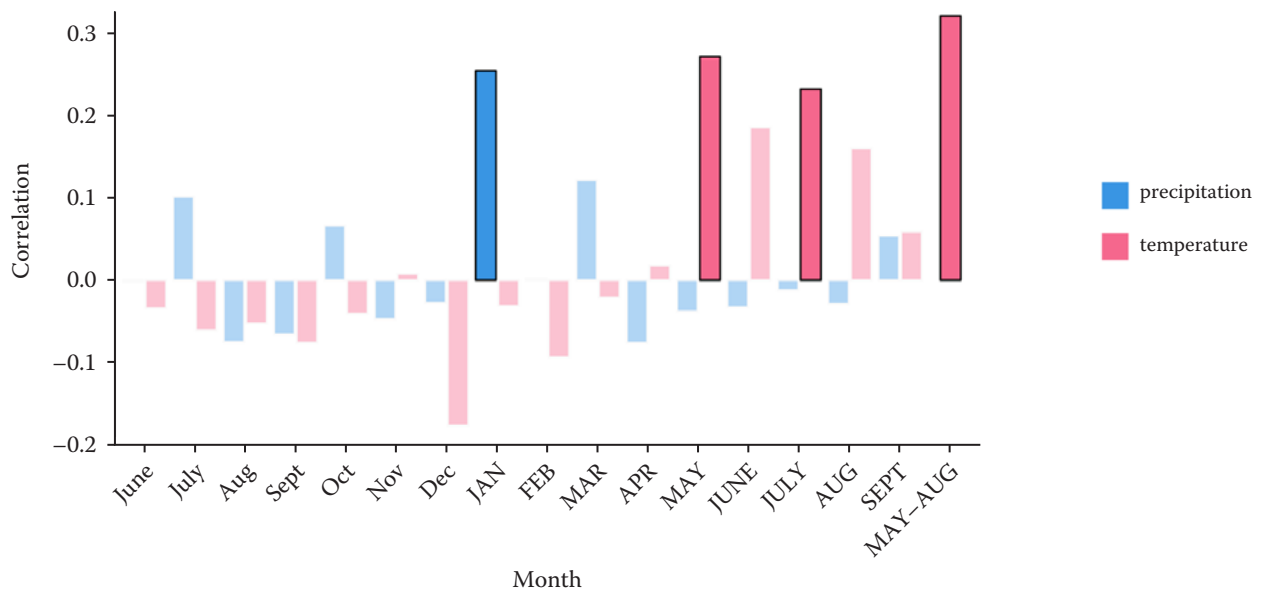


Figure 4. Climate-growth responses between tree-ring chronology and monthly mean temperature (red) or precipitation (blue) in time window 1901–2013

Solid bars with thick margins – statistically significant Pearson correlation coefficients ( $P < 0.05$ ); months in lowercase and uppercase letters are representing previous year and current year, respectively

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## DISCUSSION

**Age determination.** The determination of the age of a woody plant based on the counting of its growth rings generally underestimates its actual age compared to alternative methods (e.g. radiocarbon  $^{14}\text{C}$ ). The reason for this is the high frequency of missing rings in slow-growing shrubs and the oldest individuals in particular (Mathaux et al. 2016; Camarero, Ortega-Martínez 2019). Even though some juniper studies (Trkal, Lehejček 2017; Shetti et al. 2018a) used the serial sectioning method which supports the cross-dating efforts (Kolishchuk 1990), dendrochronology can do nothing about the fact that in climatically limited years (typically extremely cold and/or dry) not even a single row of cells is formed at the sampling spots (Speer 2010). On the other hand, Shetti et al. (2018a), based on disc scanning and ring width measurements, reported no missing rings in juniper shrubs ( $n = 30$ ) at a site near Kirkenes, which is unusual (Pellizzari et al. 2014). A reliable alternative to serial sectioning is wood anatomy microsectioning (Schneider, Gärtner 2013). It has already been successfully applied to slow-growing juniper shrubs, providing reliable results in terms of ring determination and further applications (e.g. Pellizzari et al. 2014; Lehejček et al. 2017), as it provides more detailed insight into the growth of woody plants (Schweingruber et al. 2008). Because junipers at our site grow considerably slower compared to those studied by Shetti et al. (2018a), and because growth rings often consist of a few cell rows only, we believe that the application of wood anatomy microsectioning was our only option in this study to determine and measure annual rings. Naturally, both methods can be combined (i.e. serial sectioning based on microsectioning), but this is rarely done, as it is time-consuming and laborious. Additionally, also multi-axis measurements and disc cross-dating may be applied (Shetti et al. 2018b) or more shrub samples can be harvested (Carrer et al. 2023) to increase the potential for more reliable cross-dating results and *Rbar*. Thus, it is very likely that we potentially could omit some missing rings due to cross-dating constraints probably associated with individualistic and eccentric growth in extreme conditions accentuated by heavy industrial pollution. Therefore, the shrub ages reported here have to be regarded as a conservative minimum plant life span. Nonetheless, based on our findings and to our best

knowledge, we consider our juniper growth record the longest shrub record in Scandinavia ever reported. We named the oldest individual of our record Old Juniper Troll (683 years).

**Age comparison.** Studies conducted on common juniper prove that the species can live for a very long time. Pellizzari et al. (2014) reported a 402-year-long chronology from a site in the Ventina area in the Engadine Alps. Similarly, Carrer et al. (2023) reported almost 500-year-old individuals from the Alps. Climatically more comparable to our Sør-Varanger site is the tundra environment of southwest Greenland, where one study encountered a juniper at least 350 years old (Lehejček et al. 2017). To our knowledge, only four other *Juniperus communis* chronologies from Scandinavia have been published, as summarised in Tumajer et al. (2021). These data generally indicate a shorter lifespan of populations and a distinctly lower age of the oldest individual: Abisko (mean age 85 years, max. age 323 years), Kevo (119/418), Kirkenes (98/240), Finse (66/97). Different juniper species from Scandinavia can also live notably long, as presented, for example, in Wilmking et al. (2012) for *Juniperus nana* from Abisko (mean age 53 years, max. age 174 years). *Empetrum nigrum*, another slow-growing shrub, exhibits a significantly shorter life span in Scandinavia, which is just over 60 years, as documented by Bär et al. (2008). Thus, our Sør-Varanger juniper population (190/683) is considerably older than any other shrub population from Scandinavia.

Even older individuals were found by Shiyatov et al. (2002) in the Polar Urals (*Juniperus nana*, 850 years), Camarero and Ortega-Martínez (2019) in the Pyrenees (*Juniperus phoenicea*, 927 years), or Miles and Worthington (1998) in California (*Juniperus occidentalis*, 2 675 years). Probably the oldest shrub from Scandinavia ever reported is a 940-year-old common juniper from Kevo (Kallio et al. 1971). Unfortunately, neither growth chronology nor methods accompany this single statement in the Kevo station report.

**Climate sensitivity and population characteristics.** The presented record indicates a moderate to low climate sensitivity of the population under study. Climate correlations derived from it (not shown) therefore suffer from wide confidence intervals, as our record is dominated by an individual shrub-level signal rather than a coherent stand-level signal (Speer 2010). Although shrub

chronologies can generally provide lower *Rbar* and *EPS* values, we still suggest that populations at extreme sites like ours, which consist of very old individuals often affected by large micro-site variations and exhibiting individualistic growth patterns, are a valuable source of information. Heterogenous growth of individual age classes of the population provides further explanation of low *Rbar* and *EPS* values. Similarly, Camarero and Ortega-Martínez (2019) faced issues with finding climate signals for old and slow-growing juniper populations in cliff or rocky sites. Furthermore, heavy industrial pollution – as in our case from a nickel powerplant – is known to influence plant physiology and growth (Odasz-Albrigtsen et al. 2000; Hruška et al. 2023) and thus further weakens the climate signal. We therefore suggest that old populations from extreme sites, including polluted ones, might not be useful for long-term climate reconstructions because they are likely to be influenced by a whole range of environmental conditions. Even so, however, they can still provide important material for dating studies or archaeological research.

## CONCLUSION

We have dated the oldest living shrub population ( $190 \pm 148$  years) and provided the longest shrub growth record (683 years) from Scandinavia, using the methods of dendrochronology and wood anatomy microsectioning. Ring counting, even with cross-dating, generally underestimates the age of very old individuals. It is compromised by missing rings, which is also a limitation of this study where we were not fully successful with cross-dating. We therefore present a conservative minimum age, which may be refined by alternative dating approaches. The old population of *Juniperus communis* at Sør-Varanger is only moderately climate-sensitive due to the extremeness of the site, the considerable share of old individuals in the population, their individualistic growth, and industrial pollution. All these factors compromise the utility of this population for climate-environmental reconstructions.

With respect to the increasing impacts of climate change on the environment, old junipers, which are often found beyond abiotic tree-lines in cold and/or dry environments, constitute important gene reservoirs for future shrub recruitment.

**Data availability statement.** Analyses presented and data supporting the results in the paper are available at [https://github.com/JirkaSkaut/Juniper\\_Troll](https://github.com/JirkaSkaut/Juniper_Troll) or upon request to the corresponding author.

## REFERENCES

- Adams R.P. (2008): Junipers of the World: The Genus *Juniperus*. 2<sup>nd</sup> Ed. Bloomington, Trafford Publishing: 402.
- Bär A., Pape R., Bräuning A., Löffler J. (2008): Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *Journal of Biogeography*, 35: 625–636.
- Bennett A.C., McDowell N.G., Allen C.D., Anderson-Teixeira K.J. (2015): Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1: 1–5.
- Bjerke J.W., Tommervik H., Finne T.E., Jensen H., Lukina N., Bakkestuen V. (2006): Epiphytic lichen distribution and plant leaf heavy metal concentrations in Russian-Norwegian boreal forests influenced by air pollution from nickel-copper smelters. *Boreal Environment Research*, 11: 441–450.
- Buchwal A., Rachlewicz G., Fonti P., Cherubini P., Gärtner H. (2013): Temperature modulates intra-plant growth of *Salix polaris* from a high Arctic site (Svalbard). *Polar Biology*, 36: 1305–1318.
- Bunn A. (2019): Dendrochronology program library in R: R package version 1.7.0. GitHub. Available at: <https://github.com/cran/dplR/commit/48389f3c4fd441e227d33364dcffda33eb34ba31>
- Buras A., Lehejček J., Michalová Z., Morrissey R.C., Svoboda M., Wilmking M. (2017): Shrubs shed light on 20<sup>th</sup> century Greenland Ice Sheet melting. *Boreas*, 46: 667–677.
- Camarero J.J., Ortega-Martínez M. (2019): Sancho, the oldest known Iberian shrub. *Dendrochronologia*, 53: 32–36.
- Carrer M., Dibona R., Prendin A.L., Brunetti M. (2023): Recent waning snowpack in the Alps is unprecedented in the last six centuries. *Nature Climate Change*, 13: 155–160.
- Cook E.R., Peters K. (1981): The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin*, 41: 45–53.
- Di Marco M., Ferrier S., Harwood T.D., Hoskins A.J., Watson J.E.M. (2019): Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature*, 573: 582–585.
- Fritts H. (1976): *Tree Rings and Climate*. London, Academic Press: 582.
- Harris I., Osborn T.J., Jones P., Lister D. (2020): Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, 7: 109.
- Hruška J., Oulehle F., Chuman T., Kolář T., Rybníček M., Trnka M., McDowell W.H. (2023): Forest growth responds



<https://doi.org/10.17221/118/2023-JFS>

- more to air pollution than soil acidification. PLoS ONE, 18: e0256976.
- Kallio P., Laine U., Mäkinen Y. (1971): Vascular flora of Inari Lapland. 2. *Pinaceae* and *Cupressaceae*. Reports from the Kevo Subarctic Research Station, 8: 73–100.
- Kangas J., Ollikainen M. (2022): A PES scheme promoting forest biodiversity and carbon sequestration. Forest Policy and Economics, 136: 102692.
- Keith H., Mackey B., Kun Z., Mikoláš M., Svitok M., Svoboda M. (2022): Evaluating the mitigation effectiveness of forests managed for conservation versus commodity production using an Australian example. Conservation Letters, 15: e12878.
- Kolishchuk V.G. (1990): Dendroclimatological study of prostrate woody plants. In: Cook E.R., Kairiukstis L.A. (eds): Methods of Dendrochronology: Applications in the Environmental Sciences. London, Springer Netherlands: 51–55.
- Körner C. (2017): A matter of tree longevity. Science, 355: 130–131.
- Larson D.W., Matthes U., Gerrath J.A., Gerrath J.M., Nekola J.C., Walker G.L., Porembski S., Charlton A., Larson N.W.K. (1999): Ancient stunted trees on cliffs. Nature, 398: 382–383.
- Lehejček J., Buras A., Svoboda M., Wilmking M. (2017): Wood anatomy of *Juniperus communis*: A promising proxy for palaeoclimate reconstructions in the Arctic. Polar Biology, 40: 977–988.
- Lehejček J., Trkal F., Doležal J., Čada V. (2023): Alpine and Arctic tundra shrub populations show similar ontogenetic growth trends but differing absolute growth rates and lifespan. Dendrochronologia, 77: 126046.
- Li B., Heijmans M.M.P.D., Berendse F., Blok D., Maximov T., Sass-Klaassen U. (2016): The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub *Betula nana* in northeast Siberian tundra. Polar Biology, 39: 1245–1255.
- Luysaert S., Schulze E.D., Börner A., Knohl A., Hessenmöller D., Law B.E., Ciais P., Grace J. (2008): Old-growth forests as global carbon sinks. Nature, 455: 213–215.
- Mathaux C., Mandin J.P., Oberlin C., Edouard J.L., Gauquelin T., Guibal F. (2016): Ancient juniper trees growing on cliffs: Toward a long Mediterranean tree-ring chronology. Dendrochronologia, 37: 79–88.
- Miles D.H., Worthington M.J. (1998): Sonora Pass junipers from California USA: Construction of a 3,500-year chronology. In: Stravinskiene V., Juknys R. (eds): Dendrochronology and Environmental Trends – Proceedings of the International Conference, Kaunas, June 17–21, 1998.
- Myers-Smith I.H., Forbes B.C., Wilmking M., Hallinger M., Lantz T., Blok D., Tape K.D., Macias-Fauria M., Sass-Klaassen U., Lévesque E., Boudreau S., Ropars P., Hermanutz L., Trant A., Collier L.S., Weijers S., Rozema J., Rayback S.A., Schmidt N.M., Schaepman-Strub G., Wipf S., Rixen C., Ménard C.B., Venn S., Goetz S., Andreu-Hayles L., Elmen-dorf S., Ravolainen V., Welker J., Grogan P., Epstein H.E., Hik D.S. (2011): Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. Environmental Research Letters, 6: 045509.
- Myers-Smith I.H., Elmendorf S.C., Beck P.S.A., Wilmking M., Hallinger M., Blok D., Tape K.D., Rayback S.A., Macias-Fauria M., Forbes B.C., Speed J.D.M., Boulanger-Lapointe N., Rixen C., Lévesque E., Schmidt N.M., Baittinger C., Trant A.J., Hermanutz L., Collier L.S., et al. (2015): Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change, 5: 887–891.
- Myking T., Aarrestad P.A., Derome J., Bakkestuen V., Bjerke J.W., Gytarsky M., Isaeva L., Karaban R., Korotkov V., Lindgren M., Lindroos A.J., Røstberg I., Salemaa M., Tømmervik H., Vassilieva N. (2009): Effects of air pollution from a nickel-copper industrial complex on boreal forest vegetation in the joint Russian-Norwegian-Finnish border area. Boreal Environment Research, 14: 279–296.
- NMI (2023): SYNOP data from station KIRKENES. Kirkenes, Norwegian Meteorological Institute. Available at: <https://thredds.met.no/thredds/arcticdata/obssynop.html?dataset=arcticdata/obsSynop01089> (accessed Feb 13, 2023).
- Odasz-Albrigtsen A.M., Tømmervik H., Murphy P. (2000): Decreased photosynthetic efficiency in plant species exposed to multiple airborne pollutants along the Russian-Norwegian border. Canadian Journal of Botany, 78: 1021–1033.
- Pellizzari E., Pividori M., Carrer M. (2014): Winter precipitation effect in a mid-latitude temperature-limited environment: The case of common juniper at high elevation in the Alps. Environmental Research Letters, 9: 104021.
- Pimm S.L., Jenkins C.N., Li B.V. (2018): How to protect half of Earth to ensure it protects sufficient biodiversity. Science Advances, 4: eaat2616.
- Schmidt N.M., Baittinger C., Forchhammer M.C. (2006): Reconstructing century-long snow regimes using estimates of high arctic *Salix arctica* radial growth. Arctic, Antarctic and Alpine Research, 38: 257–262.
- Schneider L., Gärtner H. (2013): The advantage of using a starch based non-Newtonian fluid to prepare micro sections. Dendrochronologia, 31: 175–178.
- Schweingruber F.H., Eckstein D., Serre-Bachet F., Bräker O. (1990): Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia, 8: 9–38.
- Schweingruber F.H., Börner A., Schulze E.D. (2008): Atlas of Woody Plant Stems: Evolution, Structure, and Environmental Modifications. Berlin, Springer: 229.
- Schweingruber F.H., Hellmann L., Tegel W., Braun S., Nievergelt D., Büntgen U. (2013): Evaluating the wood anatomy



<https://doi.org/10.17221/118/2023-JFS>

- cal and dendroecological potential of arctic dwarf shrub communities. *IAWA Journal*, 34: 485–497.
- Shetti R., Buras A., Smiljanic M., Hallinger M., Grigoriev A.A., Wilmking M. (2018a): Does sex matter? Gender-specificity and its influence on site-chronologies in the common dioecious shrub *Juniperus communis*. *Dendrochronologia*, 49: 118–126.
- Shetti R., Buras A., Smiljanic M., Wilmking M. (2018b): Climate sensitivity is affected by growth differentiation along the length of *Juniperus communis* L. shrub stems in the Ural Mountains. *Dendrochronologia*, 49: 29–35.
- Shiyatov S., Hantemirov R., Gorlanova L. (2002): Millennial reconstruction of the summer temperature in the Polar Urals: Tree-ring data from Siberian juniper and Siberian larch. *Archaeology, Ethnology and Anthropology of Eurasia*, 9: 1–5.
- Siedlecki S. (1980): Geologisk kart over Norge, berggrunnskart Vadsø, 1: 250 000. [Map]. Trondheim, Norges geologiske undersøkelse. Available at: <https://www.ngu.no/upload/Publikasjoner/Kart/B250/Vadso.pdf> (in Norwegian).
- Speer J.H. (2010): *Fundamentals of Tree-Ring Research*. Tucson, The University of Arizona Press: 333.
- Thomas P.A., El-Barghathi M., Polwart A. (2007): Biological flora of the British Isles: *Juniperus communis* L. *Journal of Ecology*, 95: 1404–1440.
- Trkal F., Lehejček J. (2017): Primary growth of *Juniperus communis* in southwest Greenland. *Biosciences in Polar and Alpine Research 2017 – Abstracts*, 7: 331–333.
- Tumajer J., Buras A., Camarero J.J., Carrer M., Shetti R., Wilmking M., Altman J., Sangüesa-Barreda G., Lehejček J. (2021): Growing faster, longer or both? Modelling plastic response of *Juniperus communis* growth phenology to climate change. *Global Ecology and Biogeography*, 30: 2229–2244.
- Wilmking M., Hallinger M., Van Bogaert R., Kyncl T., Babst F., Hahne W., Juday G.P., de Luis M., Novak K., Völlm C. (2012): Continuously missing outer rings in woody plants at their distributional margins. *Dendrochronologia*, 30: 213–222.
- Wilmking M., Buras A., Lehejček J., Lange J., Shetti R., van der Maaten E. (2018): Influence of larval outbreaks on the climate reconstruction potential of an Arctic shrub. *Dendrochronologia*, 49: 36–43.
- WinCELL (2011): *Wood Cell Anatomy*. Regent Instruments Inc. [software] Version Pro 2011. Available at: [https://regentinstruments.com/assets/wincell\\_mostrecent.html](https://regentinstruments.com/assets/wincell_mostrecent.html)
- WinRHIZO (2011): *Analysis of washed roots and arabisopsis seedlings*. Regent Instruments Inc. [software] Version Pro 2011. Available at: [https://regentinstruments.com/assets/winrhizo\\_about.html](https://regentinstruments.com/assets/winrhizo_about.html)
- Woodcock H., Bradley R.S. (1994): *Salix arctica* (Pall.): Its potential for dendroclimatological studies in the high Arctic. *Dendrochronologia*, 12: 11–22.
- Zang C., Biondi F. (2015): Treeclim: An R package for the numerical calibration of proxy-climate relationships. *Ecography*, 38: 431–436.

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