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A climate-based model to predict potential treeline position around the globe

Jens Paulsen · Christian Körner

Abstract In situ temperature measurements revealed that the position of the high-elevation treeline is associated with a minimum seasonal mean air temperature within a temperature-defined minimum season length across latitudes. Here, we build upon this experience and present the results of a global statistical analysis and a predictive model for low temperature treeline positions. We identified 376 natural treelines from satellite images across the globe, and searched for their closest climatic proxies using a climate database. The analysis included a snow and a water balance submodel to account for season length constraints by snow pack and drought. We arrive at thermal treeline criteria almost identical to those that emerged from the earlier in situ measurements: tree growth requires a minimum length of the growing season of 94 days. The model yields best fit when the season is defined as all days with a daily mean temperature >0.9 °C, and a mean of 6.4 °C across all these days. The resultant treeline model 'TREELIM' offers a robust estimation of potential treeline elevation based on climate data only. Error terms include imprecise treeline position in satellite images and climate approximations in mountainous terrain. The algorithm permits constraining low temperature limits of forest growth worldwide (including polar treelines) and also permits a bioclimatic stratification of mountain biota, for instance, for biodiversity assessments. As a side product, the model yields the global potentially forested area. The results support the isotherm theory for natural treeline formation. This completely independent statistical assessment of the climatic drivers of the global treeline phenomenon confirmed the results of a multi-year measurement campaign.

Keywords Alpine · Altitude · Arctic · Bioclimatology · Elevation · Forest · Mountains · Season · Temperature

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Introduction

The temperature limit of tree growth represents a life form boundary that separates the treeless alpine and polar tundra belt from the warmer montane and boreal belt around the globe. Except for arid and semi-arid regions, the montane belt, just as the boreal belt, is naturally forested. Situations, where appropriate substrate is lacking (e.g. eroded terrain, swamps), or where rock fall or avalanches prevent tree growth, or where forests had been devastated by fire, storms or pests or removed by human land use, are region specific or not related to biological principles that apply across the globe, and thus, cannot be predicted. Our analysis included both alpine and polar treelines.

The climatic treeline represents a most obvious land cover demarcation and its relation to temperature makes it an ideal reference line for other bioclimatic zones. Treeline is defined here as a line connecting the uppermost or most northern patches of trees of at least 3 m height in undisturbed areas (Körner 2012). This line holds a middle position between the limit of closed forests and the limit of seedling or krummholz growth beyond the treeline. Where soil moisture and the duration of the snow-free period permit, the position of the treeline is clearly related to

temperature, with a common isotherm for seasonal mean temperature of around 6 °C around the globe as will be discussed below (Körner and Paulsen 2004; Körner 2012). The reason why trees reach a low temperature limit, beyond which other plant life forms (shrubs, grasses, forbs) still thrive, has to do with the stature and height of trees, causing their canopy to experience temperatures very close to ambient air temperatures, whereas small stature vegetation can decouple aerodynamically from the free atmosphere and, thus, profit from solar heating of their canopies (Grace 1988; Scherrer and Körner 2010). The thermal disadvantage of tree stature in cold climates can be demonstrated by microclimatic data and by infrared thermography (Wilson et al. 1987; Körner 2007, 2012).

The results of 15 years of data collecting (Körner and Paulsen 2004; Körner 2012) around the globe suggest that the undisturbed high elevation and polar treelines of the world follow a common climatic envelope that makes it tempting to predict the potential treeline position by meteorological data only. Earlier attempts at delineating treeline position by temperature used proxies that work at regional or specific latitude scale only, such as the warmest month mean (e.g. Glock 1955; Holtmeier 1974; Wardle 1998) or mean annual temperature (Jobbagy and Jackson 2000) for the temperate zone. Following from our earlier works (Körner and Paulsen 2004), the position of the climatic treeline can be constrained globally by three meteorological parameters: A threshold value determines the minimum air temperature for physiological tree activity (definition of the growing season), a minimum duration and a minimum mean temperature during that season. Based on these findings, we aimed at developing a model that rests on these three parameters and predicts the potential position of the low temperature treeline from meteorological data.

Since the model described here adopts standard meteorological information at a monthly scale as provided by a global climate data base (WORLDCLIM, Hijmans et al. 2005, http://www.worldclim.org), the first assumption is that weather station data related to a certain location can be scaled to the climate trees actually experience. Over large areas and long periods, and for trees >3 m, this assumption is reasonably well supported (Körner 2007, 2012; Kollas et al. 2014). We describe the criteria by which a large data set of natural climatic treeline positions was obtained and how these positions were linked to climate data obtained from a database to 'calibrate' the model. We also describe the algorithms used to calculate the parameters needed to predict the possibility of tree growth and how we obtained the best-fit numeric values for these treeline proxies (parameterization).

The main task was to predict whether the climate at any geographical location allows tree growth or not. This offers a wide application in biogeography. One of these is a

stratification of the world into vertical (elevational) bioclimatic belts, anchored at the treeline isotherm (Körner et al. 2011). The great advantage of such an approach is the abandonment of metres of elevation or degrees of latitude as a site characterization, and rather use the actual climatic envelope. This should permit comparing mountain biota across latitudes based on bioclimatology.

Methods and model design

Basic model assumptions and definition of climatic treeline proxies

From our earlier works with data loggers (Körner and Paulsen 2004), it emerged that only three independent parameters are necessary to model treeline elevation by standardized meteorological data: (a) a threshold temperature DTMIN that constrains the growing season; (b) a minimum mean temperature for all days of the growing season SMT as defined in (a); (c) a minimum length of the growing season LGS. The definition of the growing season is a central issue, because temperatures outside the growing season have no predictive value (Körner 2012). The model, thus, needs to select periods suitable for tree growth, which means, warm enough conditions with sufficient soil moisture and no snow cover.

Defining the beginning and end of the growing season by a critical air temperature only (as in Körner and Paulsen 2004) turned out to be problematic at a global scale because this procedure does not account for irregular seasonal temperatures at equatorial latitudes, and it does not account for snow pack and drought. Therefore, the TREELIM model presented here uses a LGS representing the sum of days with a daily mean temperature above a defined threshold temperature (DTMIN). The mean temperature of the growing season (SMT) for any site is then calculated by averaging the daily means for all these days. Days during which snow is present or during which soil water is not available do not count for season length (see below). Hence, to predict the position of the low temperature limit for tree growth for a given region, the effective duration of the growing season must be known. Once this period is defined, the model takes the length of this period and its mean temperature to decide, whether tree growth is possible or not (Fig. 1).

To determine the number of days matching the criteria for the growing season (daily mean air temperature ≥ DTMEAN, absence of snow and sufficient plant available soil water) for any site, soil water content, snow melt and snow accumulation, and temperature have to be modelled on a daily basis for each day of the year. These daily data were obtained by converting the 30-year
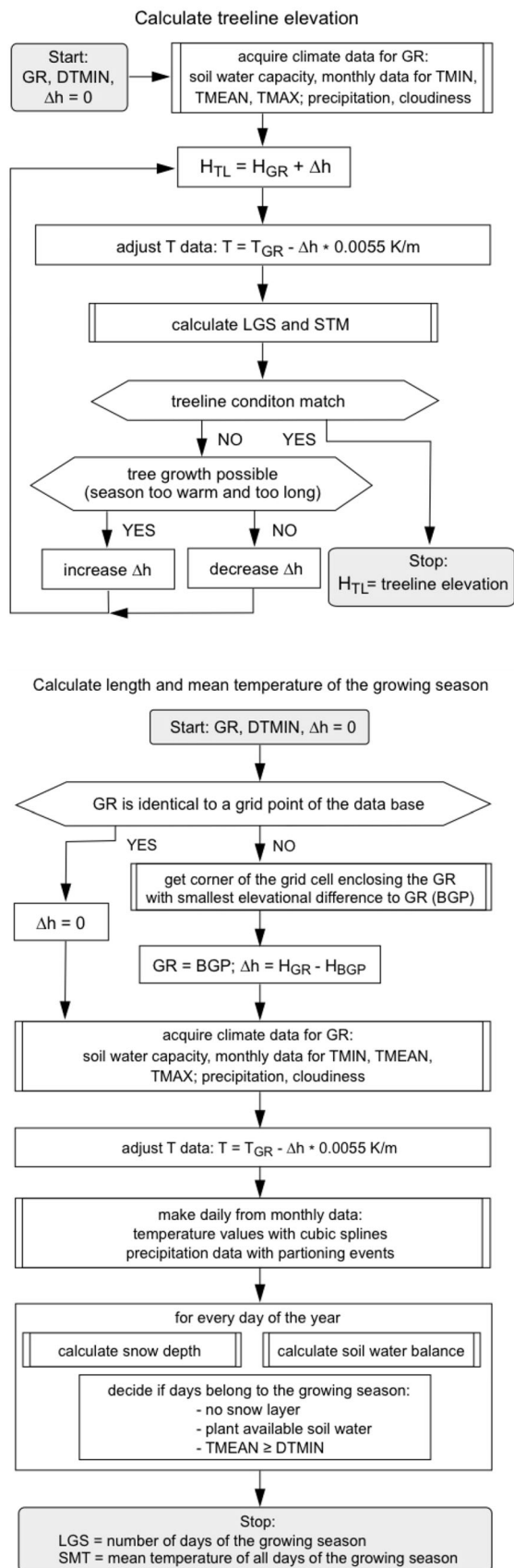
Calculate treeline elevation

Calculate length and mean temperature of the growing season

◄**Fig. 1** A schematic illustration of the main steps and modules of the TREELIM model. Subroutines that are discussed in greater detail in the text are annotated by a double line. Note, the calculation of the length and mean temperature of the growing season (LGS and SMT, *lower panel*) is a key module of the main routine (*upper panel*). GR georeference, DTMIN minimum daily mean temperature for a day to belong to the growing season, TMIN, TMEAN and TMAX monthly temperature data obtained from Worldclim, T_{GR} temperature at the elevation of the georeference, H_{TL} predicted elevation of treeline location, H_{GR} elevation at georeference, Δh elevational distance between treeline and GR. The script of the model is provided in electronic supplementary materials, S1

monthly mean temperatures from the climate data base into a seasonal course of mean daily temperatures using cubic splines. In essence, this procedure is smoothening the seasonal course of temperatures (no monthly steps) and no other assumption is made than that the shape at daily resolution matches that at monthly resolution once averaged over 30 years.

Snowpack The snow module of TREELIM accounts for the assumption that trees do not exert significant growth as long as there is late-laying snow on the ground. Snow pack may thus constrain the length of the growing period, despite warm air temperatures. It was assumed that all precipitation that falls at daily mean temperatures ≤ 0 °C fall as snow, and snow was assumed to stay and accumulate on the ground as long as daily mean temperatures remained <0 °C. If a snow layer is present, snow is assumed to melt whenever daily mean temperatures are >0 °C at a rate of 0.84 kg m^{-2} day^{-1} for each degree >0 °C (the WAT-FLOOD model; http://www.civil.uwaterloo.ca/watflood/). Sublimation was ignored.

Whenever rain falls on an existing snow layer, this water cools to 0 °C and the thermal energy (4.186 kJ kg^{-1} K^{-1}) is used to melt snow (333.5 kJ kg^{-1} snow). Thus, 1 mm of rain melts 1/80 kg m^{-2} snow per degree air temperature above 0 °C. The quantity of snow pack (in kg m^{-2}) was calculated by a simple input–output model with a daily resolution: snow layer at day (i) = snow layer at day ($i - 1$) + snowfall at day (i) − snow melt at day (i).

Because this equation is recursive, a starting point of the calculation is required. We assume that the snow layer is 0 mm at the last day of the longest consecutive period of air temperatures >0 °C. From this starting date, the snow layer submodel is run repetitively through the full year for as long as the number of snow-free days in the year changes. If the number of days without snow is 0, there is perpetual ice or snow; if not, there is at least 1 day with no snow and the quantity of snow pack is known for each day of the year.

Site water balance Since the potential treeline, by definition, is related to temperature conditions, and precipitation clearly does not exert elevational patterns that match with treeline positions across the globe, 'potential treeline' cannot

be suppresses by drought effects, but such effects can prevent trees from occurring at the potential treeline. So, while there is still a potential thermal tree limit, trees may be absent for drought reasons (arid and semi-arid regions). Hence, in the TREELIM model, water comes into play as a potential constraint to the LGS during which thermal conditions would permit tree growth.

The water balance equation was solved by a submodel of TREELIM that accounts for precipitation (liquid and solid), evapotranspiration, and the resulting soil water content. Since climate databases offer only monthly precipitation, we had to approximate actual rainfall regimes, assuming that air temperature determines saturated vapour content of the air. We then adopted a temperature-related stepwise interpolation of mean daily rainfall from annual data with a monthly resolution. This given amount of precipitation water was allocated by plausibility to precipitation events in the following way: The mean per day event was assumed to be 5 mm if the monthly mean T was <5 °C, 10 mm for 5–10 °C, 15 mm for 10–15 °C, 20 mm for >15 °C. For instance, if the monthly mean temperature is 7.3 °C and the monthly precipitation is 27.4 mm, precipitation events are assumed to be 10 mm each, one on day 7, one on day 14, and the remaining 7.4 mm are assumed to fall on day 21.

This procedure is more realistic than for instance splitting monthly precipitation into 30 events. Since soil moisture is buffering moisture availability, the actual fragmentation of monthly precipitation is not very critical, except for conditions where drought is critical, which is rare at alpine treeline elevations. Errors introduced by this procedure are certainly small compared to the uncertainty of actual precipitation at treeline, based on climatic layers derived from low elevation climate stations.

Daily *Potential evapotranspiration* (DPET) was estimated using the Hargreaves equation (Hargreaves and Samani 1985) in the FAO-56 form as adopted by Allen et al. (1998), again with a daily resolution. Input variables are the elevation of the site, daily maximum and minimum temperature derived from WORLDCLIM data, solar radiation (depending on season and latitude) and cloudiness data obtained from the University of East Anglia Climatic Research Unit (CRU; http://www.cru.uea.ac.uk; New et al. 2002). We calculated solar radiation with the equations provided by the University of Oregon Solar Radiation Monitoring Laboratory (http://solardat.uoregon.edu/SolarRadiationBasics.html).

The water balance for a given day was then calculated with a two-layer bucket model for a given soil water holding capacity as defined by the International Geosphere-Biosphere Programme (IGBP 2000). We assumed an upper soil layer that holds a maximum of 30 mm of water (or less if the IGBP value was less than these 30 mm), and a lower layer with a water holding capacity for the remaining profile as indicated in the IGBP data minus the 30 mm for the upper layer. As long as water was available in the upper layer, daily evapotranspiration was assumed to equal potential evapotranspiration. If the upper layer was water saturated (more than 30 mm H_2O), any additional rain or snow melt water flows into the lower soil layer until it is also saturated, and any extra water creates runoff. Once the upper layer becomes dry, we used a simple square root correction for the estimation of the real daily evapotranspiration (DRET) from deeper layers, accounting for the diminishing uptake by roots from drying soils and the growing resistance to water diffusion through the dry upper soil layers, as proposed in the WATFLOOD model (http://www.civil.uwaterloo.ca/watflood/): DRET = DPET × (actual soil water content/soil water capacity)$^{1/2}$ in kg m^{-2} day^{-1}, with soil water values in kg m^{-2} (Donald et al. 1995; Kouwen et al. 2005). The equation is recursive, and the model starts its first run at the last day of the driest period (the longest period without precipitation and the highest accumulated potential evapotranspiration) with an actual soil water content that is half its field capacity. The model is then run until the actual soil water values for each day of the year are stabilizing, i.e. do not change from one year to the next. Because DRET is always less than the actual soil water content, the actual soil water content is always >0 and the drought limit for tree growth was assumed to be at 20 % of field capacity.

Combining the sub-routines These routines will become particularly effective in areas where there is a likelihood that snow pack or drought constrain the season length below a critical number of days, and they are constraining the actual number of days that belong to the growing season as determined by temperature only, and with this, these routines are influencing the resulting mean temperature for that period (the number of days from which the critical seasonal mean temperature is calculated). After processing these routines, for every day of the year the presence or absence of snow, the actual soil water content and the mean air temperature are known and the length and the mean temperature of the growing period can be calculated.

Because we use an annual course of daily temperature that resulted from smoothing a 30-year mean monthly course of annual temperature, the temperature thresholds are generally passed only once in spring and once in autumn (except for equatorial latitudes). Cold events during the growing period are averaged out in the long-term means, despite the fact that summer snowfall is common in climates near higher latitude treelines. This also applies to dry episodes in regions with a humid climate. SMT is the mean air temperature of all days that are contributing to LGS. If LGS is zero (because no day is warm enough, or because of arid climate, or because of the presence of perpetual snow) SMT is not defined. Applying such long-term means is very realistic in the light of the long integration periods encountered in treeline formation.

As an example, Fig. 2 shows the modelled key parameters for a moist high montane climate (LGS = 168 days, SMT = 9.3 °C for DTMIN = 0.9 °C). It also shows that the start of the growing season could be delayed by more than 2 months by late snow pack, while the end is determined by low air temperature.

In regions with one or more dry seasons, the growing period may additionally be fragmented by soil drought. The example shown in Fig. 3 shows that the short growing period in spring is only made possible because the winter snow layer accumulates the scarce precipitation: it starts after snow melt and ends by the time the soil moisture is exhausted. A second growing period in autumn may be too short for significant growth, but could contribute to the formation of storage reserves in trees.

Climatic proxy data for actual treeline position

The modelling hypothesis assumes that trees are able to persist if the snow-free and sufficiently moist part of the season reaches a minimum warmth and length. In other words, the value for seasonal mean temperature (SMT) must not fall below a certain seasonal mean temperature SMTMIN, and the LGS must not be shorter than a minimum season length (LGSMIN). In the following, it is explained how numeric values for DTMIN, LGSMIN and SMTMIN were obtained.

Trees can grow if the season is long and warm enough. The threshold values (LGSMIN and SMTMIN) are identical for all sites (no regional bias). This translates to the Boolean expression SMT ≥ SMTMIN AND LGS ≥ LGSMIN to be true for all sites where trees can grow. At the climatic limit of tree growth, i.e. at the treeline, the expression changes to (SMT = SMTMIN AND LGS ≥ LGSMIN) OR (SMT ≥ SMTMIN AND LGS = LGSMIN) depending on the climate character, causing either season length or SMT to first constrain tree growth.

Changing the temperature data for a site will shorten or lengthen the duration and mean temperature of the growing season. Air temperature is correlated to elevation by the lapse rate. Altering the temperature data by a constant value is equivalent to a shift of the elevation of the site. An elevation can be calculated where the above logical expression for season length and SMT match. This is the predicted treeline elevation for a given site. If this calculation is done for a site known to be at the treeline, and if the values for DTMIN, SMTMIN and LGSMIN are correct, the calculated treeline elevation should match the real one. If done for many treeline sites, the remaining mean error in elevation is a measure of the appropriateness of the numerical values of DTMIN, SMTMIN and LGSMIN.

We used a set of 376 treelines sites. These sites have been located using Google Earth satellite images
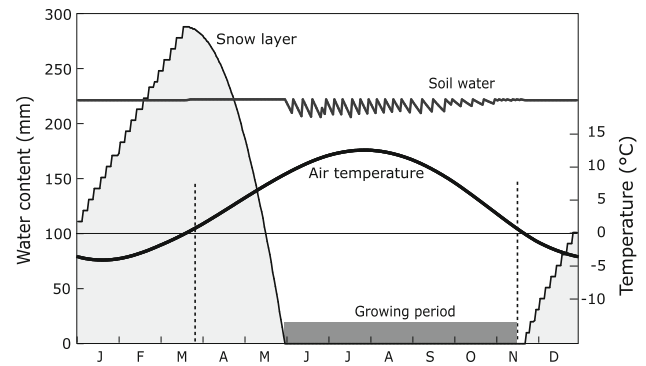

Fig. 2 An example of modelled annual snow layer (mm water) and soil water content for a high montane site (47°15′N, 9°45′E, 1,417 m a.s.l) with perhumid climate. The *dotted vertical lines* indicate the limits of the growing season as set by air temperature only
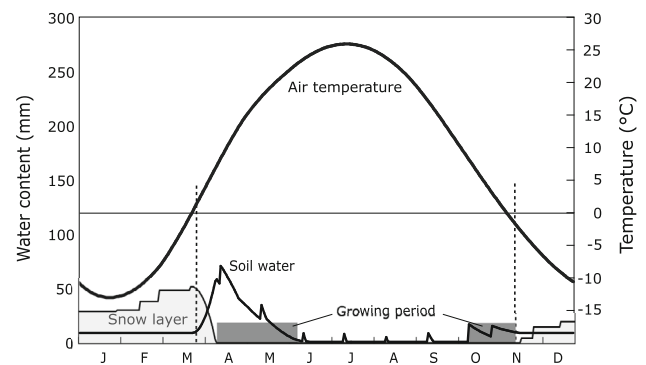

Fig. 3 An example for the modelled annual of snow layer and soil water content for a continental site (47°15′N, 62′E, 62 m a.s.l.) with steppe climate. The *dotted vertical lines* indicate the limits of the season as set by air temperature only

(Fig. 4). We scanned Google Earth for clearly recognizable treeline positions in regions where the quality of the images was good enough, and with large enough montane forest areas that permitted to identify the most likely upper or most northerly limit of groups of trees (Fig. 4). Since Google Earth offers continuous readings of site elevation (as one moves the cursor), it is easy to search for maximum elevation of trees in a given region. The accuracy of Google Earth elevations compared to the elevation values given in Worldclim tested for 144 random points across the globe was: $\Delta h = 3.7$ m $\pm$ 52 (SD). Determining treeline elevation using satellite images incurs some uncertainties. These images do not always permit to distinguish between tall shrub and trees, and there always remains some uncertainty with regard to regional land use and thus anthropogenic effects. We carefully scanned the whole region of a site before accepting a site as a 'natural' climatic treeline to avoid sites with local treeline depression by any sort of
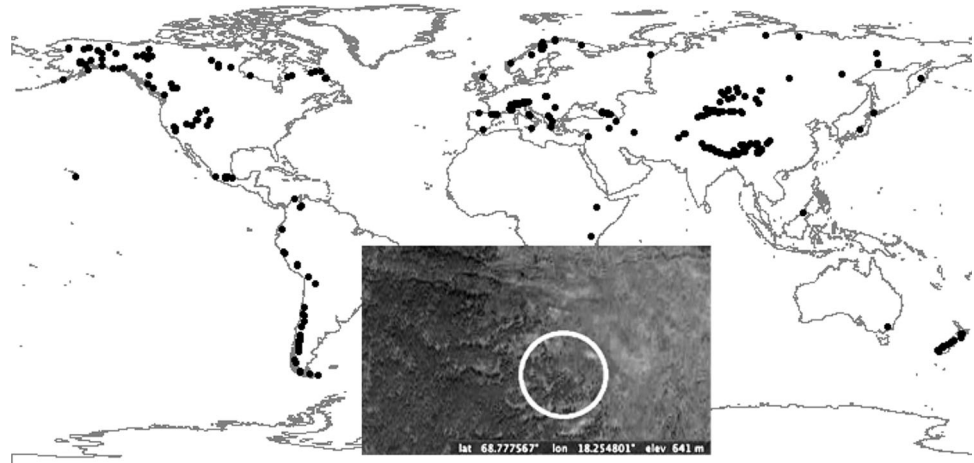
disturbance, a procedure similar to the one adopted by Paulsen and Körner (2001).

We used WORLDCLIM 1.4 at 2′30″ resolution and Mercator-projection (WGS84) for topography, air temperature and precipitation (data at monthly resolution). The 2′30″ of the used WORLDCLIM database grid corresponds to 4.6 km in latitudinal direction and to 4.6 km times the cosine of latitude in the longitudinal direction (i.e. 4.6 km at the equator and 3.3 km at 45° N or S).

We calculated the climate assumed to prevail at the selected treeline location from that grid point of the WORLDCLIM pixel containing this location that came closest to the elevation of the test site. The remaining elevational distance was accounted for by assuming a common altitudinal lapse rate of air temperature of -0.0055 K m^{-1} during the growing season (Körner 2012).

For each of the 376 treeline sites, we tested any possible combination of DTMIN, SMTMIN and LGSMIN to find the smallest deviation between modelled potential versus actual treeline elevation. Specifically, we assume values for DTMIN and SMTMIN in 0.1 K steps (note the use of K for temperature differences and °C for temperatures), and LGSMIN in 1-day steps. There are $(8 - 0 \,°C)/0.1 \text{ K} \times (8 - 0 \,°C)/0.1$ K/2 $\times$ (150 – 60 days)/1 day = 288,000 combinations: there are forests where the daily mean air temperature never reaches 8 °C, and where the season is shorter than 150 days. For each of these combinations of values for DTMIN, SMTMIN and LGSMIN, we calculated the treeline elevation of the 376 calibration points, and the residual error in terms of (elevation predicted − elevation measured) was used to rate the appropriateness (fitting) of the three core parameters. The value triplet with the lowest error was then chosen to predict treeline elevation from meteorological data. The remaining error indicates the limitations of the model and the available data.

Results

The resultant parameters that yielded the best approximation of treeline elevation globally, are 0.9 °C for DTMIN, 94 days for LGSMIN, and 6.4 °C for SMTMIN. The TREELIM model reproduces some well-known phenomena related to treeline position such as the lack of forest in regions with <200 mm annual precipitation irrespective of the climate zone, the depression of treeline elevation with increasing precipitation (typically near the equator and in coastal areas and moist mountain ranges), and the maximum elevation of potential treeline in relatively dry mountains of the subtropics of both hemispheres (Fig. 5). The regression inserted in Fig. 5 illustrates the performance of TREELIM with a root mean square error (RMSE) of 78 m for the predicted versus the actual treeline. As an example, we offer an analysis at a regional scale for New Zealand, where treeline elevation is predicted by TREELIM with a mean error of 11 m (Table 1).

Extended beyond mountainous terrain, for which TREELIM was designed, the model also yields the potential global forest area based on climate only (Fig. 6). Surfaces labelled as 'arid' are treeless (too dry for tree growth). Note, the vegetation categories emerging from TREELIM cannot be expected to match classical biome categories, because we use strict climatological criteria rather than statistical proxies for certain vegetation types. The total potential forest area globally arrives at 88 Mio km^2 of which 12 Mio km^2 is montane (Körner et al. 2011), 58 Mio km^2 is potentially covered by boreal, temperate, subtropical and seasonal tropical forests, and 18 Mio km^2 fall in the perhumid tropical regions. 33 Mio km^2 are too dry for tree growth at any elevation, although temperature alone would not prevent tree presence (Table 2).

Fig. 5 Modelled (potential) and actual treeline position for 376 treeline sites across the globe (see Fig. 4). The variation at a given latitude largely reflects the regional climate variation at same latitudes (e.g. oceanic vs. continental climate). The difference between actual and predicted treeline, any errors in the climate proxies obtained for that location, and its elevation and the intrinsic limitations of the model. The *inset* shows the accuracy of the model at different elevations of the treeline (elevation predicted = 1.005 × elevation measured − 1 m, $r^2 = 0.997$, RMSE = 78 m)
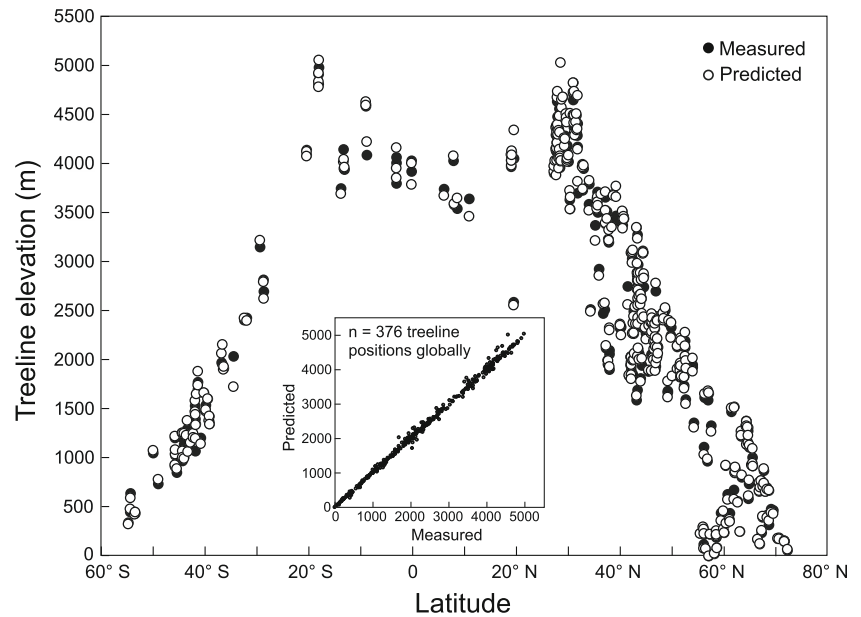

Table 1 The potential climatic treeline in New Zealand as predicted by the TREELIM model

Latitude	Longitude	Exposure	Treeline elevation measured (m)	Treeline elevation predicted (m)	Treeline elevation predicted minus measured (m)
−45.452297	166.964312	E	854	893	39
−45.821247	167.064713	NE	914	932	18
−45.746002	167.435498	N	1,077	1,086	9
−44.419006	168.100470	N	1,210	1,256	46
−44.397979	168.820244	S	1,053	1,073	20
−44.048663	168.848888	SE	1,011	995	−16
−44.066847	168.893085	NW	1,139	1251	112
−43.626258	170.271241	SE	1,261	1,231	−30
−43.349191	170.555730	W	1,121	1,065	−56
−42.863887	171.529996	S	1,100	1,157	57
−42.331892	172.079341	NE	1,240	1,210	−30
−42.333333	172.083333	NE	1,220	1,251	31
−41.952443	173.047347	SE	1,478	1,472	−6
−41.967142	173.047670	N	1,535	1,586	51
−40.830681	175.415764	NW	1,205	1,147	−58
−39.272947	175.501629	W	1,379	1,383	4
−39.166667	175.850000	NW	1,350	1,344	−6
−39.207596	175.874502	NW	1,424	1,429	5
Mean deviation					11

We applied the global algorithm to 18 regional, undisturbed treeline positions. We attribute the local deviations in elevation to the deviation of the WORLDCLIM climatic layer from actual site conditions

Latitude and longitude in decimal °

Sensitivity of the model

To test the sensitivity of the model, we calculated the net effect of an error in treeline elevation on the potential forest covered area (Fig. 7). Figure 7 shows that, at the elevation of the climatic treeline, the land surface area is ca. 17'000 km² per m of elevation. Hence, an elevation error of 100 m would produce ca. $100 \times 17,000$ km² = 1.7 Mio km² of change in uppermost montane forest area. If the model placed the treeline systematically at a 0.55 K

Position relative to treeline
- far above
- adjacent above
- adjacent below
- below
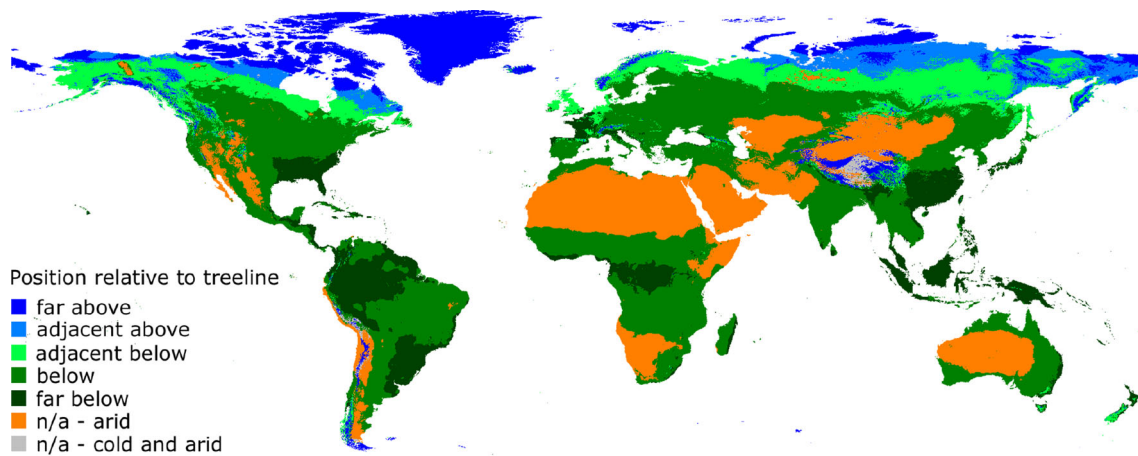- far below
- n/a - arid
- n/a - cold and arid

Fig. 6 World map of potential land cover relative to climatic treeline position (see also Table 2). Surfaces labelled as 'arid' are too dry for tree existence, but trees would grow if irrigated or in depressions where water accumulates. Surfaces labelled as 'cold and arid' are both too dry and too cold for tree growth (e.g. parts of Tibet and of the South American Altiplano)

Table 2 Potentially forested area relative to treeline position (land area without Antarctica)

Climate code	Land area (Mio km^2)	Type of potential vegetation
1	8.41	Cold desert or cold semi-desert
2	5.42	Alpine grassland and tundra
3	12.16	Montane or boreal forest
4	58.07	Temperate and subtropical forests
5	17.78	Perhumid, no frost
6	31.88	Hot desert or semi-desert
7	0.92	Dry and cold desert or semi-desert

Climate codes: 1 (far above treeline): season length (LGS) ≤30 days or season mean temperature (SMT) ≤3 °C; 2 (adjacent above treeline): 60 days < LGS < 94 days and 3 °C < SMT < 6.4 °C; 3 (adjacent below treeline): 6.4° ≤ SMT ≤ 10° and LGS ≥ 94 days or 94 days ≤ LGS ≤ 130 days and SMT ≥ 6.4 °C; 4 (below treeline): growing season warmer and longer than (3), but drought or frost or both occur; 5 (far below treeline): perpetual growing season; 6 (hot and arid): too dry for tree growth; 7 (cold and arid): too cold, but also too dry for tree growth (for instance parts of western Tibet)

(+100 m) too cool position, or if climate warming would shift treeline corresponding to an increase of temperature by +0.55 K, the potentially forested land area would be +1.7 Mio km^2 (1.9 %) larger, not accounting for fire or any other forest disturbance. This number reflects the net effect of a thermal stimulation of tree growth and (to a small extent) enhanced water stress (in very dry regions).

The model clearly shows that high precipitation is negative for treeline elevation, with highest treelines in relatively dry regions. Hence, above a certain threshold, treeline is depressed by increasing precipitation, as exemplified for the temperate zone in Fig. 8. That trend is well reflected in the central versus front range elevations of treeline and has to do with either greater snowpack or cloudiness (part of which is known as the mass elevation effect, Brockmann-Jerosch 1919; Körner 2012).

Discussion

The position of the low temperature limit of tree growth can be predicted globally by a common set of climate parameters. The treeline phenomenon appears to have a common biological cause that applies across climatic zones (latitudes). Based on a broad set of reference points at the treeline and climatic information obtained from a public database, we arrived at very similar climate proxies like those obtained from in situ data using data loggers (Körner and Paulsen 2004 and additional data collected since then, see Körner 2012). The best fit for minimum season length in our model is 94 days (compared to the 90 days obtained from field measurements), and the best fit for the minimum mean temperature is 6.4 °C (compared to 6.5 °C in the earlier assessments). These new parameters reflect both, the wider sample of locations as well as the deviations of spatially interpolated WORLDCLIM data from actual treeline temperatures as recorded by data loggers. Based on both independent assessments, the potential treeline can be reasonably well predicted with these climatic descriptors. We believe the remaining error in elevation is also a result of WORLDCLIM climatic layers missing exact local temperatures, an error intrinsic to any model using a climate data base (see below).

Because of 20th century global warming, the temperatures used by WORLDCLIM (commonly calculated from data measured in the years 1950–2000) do already reflect the early part of the global rise in temperature (perhaps 0.3–0.5 K). Hence, had the actual treeline been tracking

Fig. 7 Land area by elevation relative to the position of the regional potential climatic treeline (without Antarctica). The area right of the dotted line includes the alpine and nival biogeographic belt and the arctic tundra. The area immediately *left* of the *dotted line* is the montane or boreal forest belt, with the land furthest below the treeline to the *left* end
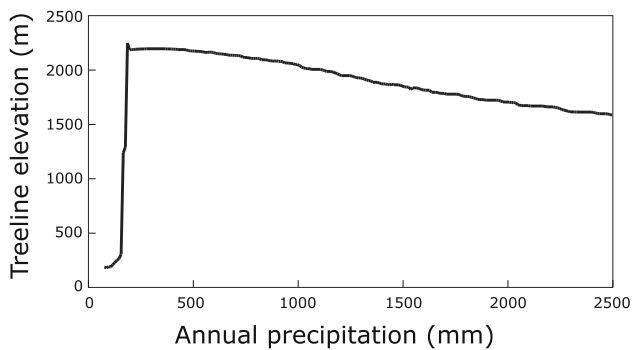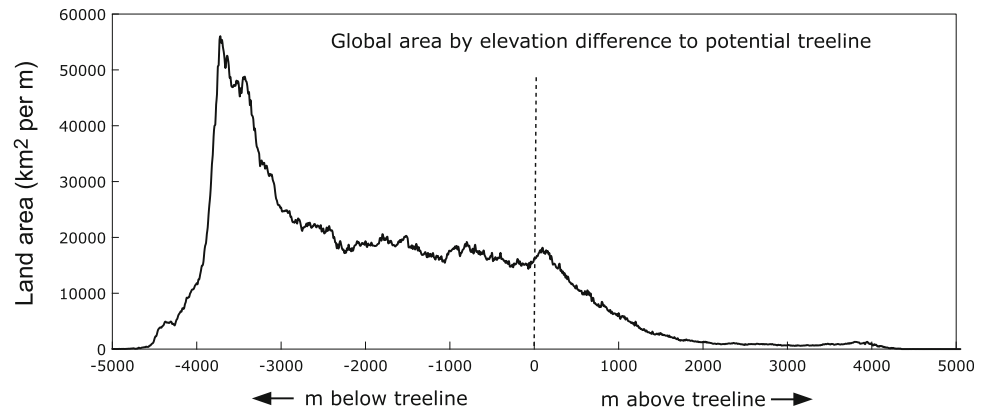

Fig. 8 Predicted treeline elevation for a temperate zone treeline site (47°15′N, 9°45′E), if the climate is modified by varying annual precipitation only (under otherwise constant temperature conditions). The higher the precipitation, the lower the treeline

these changes, the treeline would be at a 60–90 m higher position. Given the ongoing warming, more recently collected temperatures would be differing from those at the potential tree limit even more, simply because tree responses lag behind climatic changes, and the current treeline position is a legacy of past climates (Körner 2012). We may, thus, assume that the isotherm for seasonal temperature is closer to 6.0 °C (or even slightly below) in a steady-state treeline–temperature equilibrium. This may be one of the reasons, why some tropical treelines showed slightly lower SMT values than some mid latitude treelines (the humid tropical ones likely to be closer to thermal equilibrium because of less pronounced warming in low compared to high latitudes).

There are some intrinsic limitations to a climate-based modelling of potential treeline position as attempted here. We need to assume that the available data are of the same quality across the terrestrial surface. Had we used better data available for some countries only, predicted treeline elevation would be better constrained in these regions (as in the example for New Zealand shown in Table 1). Hence, a major source of error is that the density of climate stations commonly gets scarce in mountain regions. The climate approximations get weaker and the sometimes

rapid change of precipitation over short horizontal distances is not reflected in the climate database. Other local climatic peculiarities such as shelter effects of mountains (lee versus luv climates), local wind systems such as Föhn wind or cold air drainage, summit syndromes (isolated mountain tops, cloudiness), etc. may also contribute to this type of error. Soil moisture approximations are always a problematic part in modelling plant water relations because the available soil data are close to guessing in mountain terrain, and rooting depth is unknown.

Because modelling precipitation in mountain regions from scarce weather stations is an error-prone task (Hijmans et al. 2005), we believe that the inaccuracy of precipitation data and their effect on snow pack is a major source of the remaining error of the model at a local scale in very humid regions. With these limitations, the model predicts potential treeline compared to actual treeline by a root mean square error (RMSE) of 78 m (Fig. 5). Hence the model has high predictive power at large geographical scales and for regions with highly constrained climatic information, and it should not be expected to predict the position at a local scale, particularly not for regions with very few climatic stations. Yet, as the example for New Zealand (Table 1) shows, the predictive power can even be higher at a regional scale (11 m mean error) despite parameterization was obtained from global data.

Other limitations are relatively simple routines for processes like snow melt and evapotranspiration. While WORLDCLIM uses regionally and seasonally variable temperature lapse rates, we used a uniform temperature lapse rate of -0.0055 K m^{-1} across the globe for scaling over the remaining distance from a WORLDCLIM grid point to treeline elevation. Since this commonly incurs only a few hundred metres, a regional deviation of the lapse rate should hardly affect the resultant treeline position. Some of the variations seen in Fig. 5 may relate to such effects. This kind of noise cannot simply be reduced by sampling more treeline sites, because the error is intrinsic to the available climate data. Simplifications in the

modelling algorithms would affect all sites similarly (systematic deviation from reality). However, the surprisingly close matching of the results with an independent earlier assessment by in situ data loggers (Körner and Paulsen 2004, plus data collected since then, Körner 2012) suggests that such systematic errors are very small at a global scale (but may be substantial locally).

A common isotherm of low temperature for forest limits worldwide, as this assessment revealed it, calls for a common mechanism. This is not the place to re-review this field (see Körner 2012). However, it is worth re-calling the range of environmental contrasts such an isotherm-related treeline passes through at a global scale. Forest limits are found between sea level and 5,000 m a.s.l., corresponding to an almost halving of atmospheric pressure and, thus, CO_2 partial pressure, with only a minor fraction of the photosynthetic disadvantage of increasing elevations (at similar temperature) balanced by enhanced gas diffusivity (Körner, 2012). Further, the isotherm includes locations from 94 up to 365 days of growing season length, i.e. a two- to threefold contrast in annual potential photosynthetic assimilation, if one accounts for the fact that high latitudes offer longer days.

There is also a lot of physiological evidence, that carbon acquisition (photosynthesis) is far less sensitive to low temperature than structural carbon investment (biomass production), hence, carbon limitation is an unlikely global driver of low temperature forest limits (see Körner 2012; Hoch and Körner 2012). Modelling forest growth in cold climates based on photosynthesis responses lacks a biological justification, although such models may arrive at approximations for reasons related to parameter selection and tuning (rather than reflecting actual mechanisms; e.g. Schwalm and Ek 2004). Similar to drought (for a review see Muller et al. 2011), low temperature affects tissue formation directly, and does not permit significant biomass accretion at temperatures below 5 °C (Rossi et al. 2007; Alvarez-Uria and Körner 2007), a well-known threshold in agriculture (e.g. for winter crops; Körner 2008). Such thermal thresholds act instantaneously on life processes. Thus, daily, monthly or even seasonal means cannot capture such biological limits.

Hence, the obtained isotherm must not be interpreted as a physiological threshold for certain vital processes, but rather reflects an arithmetic mean that is subsuming the combined action of low temperature, integrated over time, on a suite of processes associated with tissue formation, from root tips to apical meristems. The fact that the mean 6.4 °C growing season temperature limit comes close to known physiological growth limits should not distract from the actual situation in the field, where temperatures may vary greatly (e.g. from −5 to +25 °C during the growing season), thus including many warm hours. There is great

seasonal variation of temperature in some (temperate and subtropical) but not in other regions (humid tropical). When temperatures were allowed to vary experimentally in a day–night regime between 0 and 12 °C versus a constant 6 °C temperature, the growth rate of seedlings of treeline conifers was not different (Hoch and Körner 2009) and the effect of low temperature could not be compensated by fertilizer addition (Hoch 2013). These results hint at some trade-off between rate and duration of growth at a diurnal scale, but not at an annual scale, given the similar isotherms across latitudes (and season lengths). Research is needed to decipher the causalities behind a seasonal mean temperature threshold for treeline, given that most biological processes show a non-linear response to temperature.

The global potential forest cover presented in Fig. 6 is a side product of predicting the high elevation tree limits across latitudes. Despite its simplicity, this model offers a very realistic picture of potential global land cover by forests. As temperature becomes uncritically warm, the routines employed for water will gain more weight as they have at treeline, and we expect that drought limits of tree growth will be mirrored less precisely by our routines at low elevation. The global potential forest area of 88 Mio km^2 (83 % of vegetation covered land, 65 % of all land outside Antarctica) obtained here, covers a larger area than the actual forest covered area.

The problem with any actual forest area estimates is the completeness of cover. Some statistics count 1° × 1° pixels as bearing forest as long as at least 5 % of the grid area carries trees (DiMiceli et al. 2011). Others use thresholds between 10 and 30 % per grid cell to be considered forested (Zomer et al. 2008). Saugier et al. (2001) accumulated data for tropical (17.5 Mio km^2), temperate (10.4 Mio km^2) and boreal forests (13.7 Mio km^2; total 41.6 Mio km^2) that can be considered more or less 'closed'. However, their 'savanna' category (27.6 Mio km^2) is largely grassland as result of fires (Bond et al. 2005). To estimate the savanna forest fraction, we assumed that undisturbed savannas could bear a biomass stock corresponding to the global average for forests (between very low, boreal and very high, tropical), and compared this estimate to the actual savanna biomass pool listed by Saugier et al. (2001), which yields a ca. 24 % forest fraction of savannas, or 6.5 Mio km^2, bringing the global forest area on a close-to-full cover basis to 48 Mio km^2 or 45 % of the 106 Mio km^2 that are not deserts or covered by ice (hence bear some vegetation). The fraction would fall to 36 % if all land area outside Antarctica (ca. 135 Mio km^2) would be used as a reference. An actual forest area of 48 Mio km^2 corresponds to 55 % of the potential forest area predicted by our model (45 % loss of forest). Bond et al. (2005) assumed a potential 56 % cover of land area by forests (but they do not mention what their 100 %

reference is). For that land area fraction, they estimate that the actual forest area is only half as big as a result of fire (27 %). Hence, applied to our 88 Mio km^2 of potential forested land, the actual forest cover would arrive at 42 Mio km^2, an area exactly as big as the ca. 42 Mio km^2 listed by Saugier et al. (2001) for tropical, temperate and boreal forests (excluding savannas).

The TREELIM model is climate-driven only, hence, it applies to any low temperature treeline, including the arctic one. If the global land area considered is confined to rugged terrain (sensu mountains; for ruggedness see Körner et al. 2011), the strictly speaking 'montane' fraction of cool climate forests covers potentially 7.1 Mio km^2 or 43 % of the global total mountain area of 16.5 Mio km^2 as defined by ruggedness. These examples illustrate the usefulness of a bioclimatic definition of the low temperature treeline in global land cover statistics (Körner et al. 2011).

In conclusion, with TREELIM, we offer a new tool to predict the natural (climatic) high-elevation and high-latitude treeline. With this climate-driven biogeographic boundary, other bioclimatic zones can be defined relative to treeline position, thus avoiding the latitudinal bias of elevation in metres. Finally, this model strengthens the evidence for a common biological cause of the potential treeline position. The model cannot cover stochastic phenomena such as absence of trees from the potential treeline for reasons of disturbance, lack of substrate or the regional lack of suitable taxa. A single, relatively simple algorithm permits the prediction of potential treeline position across climatic zones.

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