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Mass elevation effect and continentality have a stronger impact on global treelines than spatial isolation

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Abstract

Aim: The global relationship between treeline elevation and temperature (or latitude as a proxy) is well established. However, additional large-scale and regional abiotic influences such as mass elevation effect (MEE), continentality and isolation are superimposed onto the latitude-treeline relationship. To quantify these effects, we apply globally applicable measures and test the effects of MEE, an aspect of continental climate and isolation on treeline elevation.

Location: Global treeline elevations ($n=629$).

Methods: We sampled treeline sites using earth observation. We calculated MEE as the distance to the nearest mountain chain limits. Continentality was assessed by the distance to the nearest coastline. Isolation was calculated by the nearest distance of a mountain chain to another mountain chain within a comparable elevational band.

Results: The global latitudinal pattern showed a distinct bimodal latitude-treeline elevation relationship. Treeline elevations increased substantially with increased MEE and distance to coastlines while isolation even decreased treeline elevations.

Main Conclusions: Our study shows a globally consistent effect of MEE and distance to the coastline on treeline elevation, contributing to our basic understanding of large-scale biogeographic processes governing treeline formation. MEE and continentality reduce cloudiness and increase solar radiation, resulting in higher treeline elevations. Isolation effects are not consistent and may be influenced by immigration and speciation. Understanding global treeline formation using comprehensive measures contributes to a better understanding of how environmental conditions determine vegetation boundaries at large spatial scales.

KEYWORDS
biome, continentality, isolation, mass elevation effect, Massenerhebungseffekt, treeline

1 | INTRODUCTION

Alpine treelines are one of the most prominent natural borders between ecosystems. The alpine treeline is characterized by sharp ecotones and short dispersal distances, in contrast to the arctic treeline between the zonal biomes of boreal forest and tundra (Körner, 2012). However, both separate tree-dominated ecosystems from treeless ecosystems characterized by perennial grasses and clonal dwarf shrubs (Körner, 2012). Such obvious structural borders have attracted the interest of ecologists and biogeographers for centuries and are represented in a legacy of seminal classic studies (Ellenberg, 1966; Hermes, 1955; Holtmeier, 2003; Körner, 1998; Schröter, 1908; Tranquillini, 1979; Troll, 1948; von Humboldt, 1808). Holtmeier and Broll (2020), so far, made the largest review on treeline research, giving an overview of changes and trends in treeline research. Recent treeline studies focus on treeline dynamics (e.g., Beloiu et al., 2021; Hansson et al., 2021; Harsch et al., 2009; Jacob et al., 2015), treeline ecotone (e.g., Bader et al., 2021) or treelines on islands (e.g., Irl et al., 2016; Karger et al., 2019). Temperature-related growth limitations of trees at the treeline are currently the best-supported explanation of the global treeline (Case & Duncan, 2014; Irl et al., 2016; Körner & Paulsen, 2004; Troll, 1961). Körner (1998, 2007) presents minimum temperatures as a fundamental limit of plant growth: Compared with shrubs and herbs, trees can benefit less from favourable microclimatic conditions close to the ground because they experience more days below a minimum growth temperature as a result of their growth height and stronger atmospheric coupling. Thus, the treeline reflects an isotherm that wraps around mountains at the upper end of the physiological limit of tree growth.

All current empirical studies support the latitudinal-bimodal relationship of treeline elevation (Paulsen & Körner, 2014; Zhao et al., 2015), which fits to the classic global treeline gradients illustrated by Troll (1948). This latitudinal-bimodal relationship can be seen as a rough proxy for the underlying limit of a minimum growth temperature as proposed by Körner (1998). Obviously, there is a wide scatter of realized treeline elevation within a given latitude (Paulsen & Körner, 2014; Zhao et al., 2015) which leads to the question, which additional ecological drivers modify global treeline patterns. Körner (1998, 2007) explains the abiotic physical limit at treelines very clearly based on the tree growth enabling temperature (Figure 1a). Consequently, we integrate this approach as the potential global treeline.

We propose three additional spatial drivers (i) mass elevation effect (MEE), (ii) distance to coastlines and (iii) isolation (Figure 1b–d) that can modulate the global latitudinal-bimodal relationship of treeline elevation indirectly via the growing temperature (i and ii) or directly by limiting the treeline species pool (iii). Doing so, we incorporate MEE and distance to coastlines as proxies modulating the regional climate, and isolation as a spatial factor influencing speciation and migration of treeline-forming tree species.

The MEE was introduced as the 'Massenerhebungseffekt' over a century ago (Brockmann-Jerosch, 1919; Schröter, 1908). This term describes the phenomenon that thermoclines tend to increase towards the centre of mountain chains leading to an upward shift of vegetation belts (Flenley, 2007; Grubb, 1971; Zhang & Yao, 2016). The MEE is one aspect of continental climate and will increase with the spatial extent of high mountain chains. Causes for the MEE are reduced cloudiness, enhanced solar irradiation and therefore higher temperatures at a given elevation and latitude in the centre of mountain chains compared to single mountain peaks or treelines in proximity to the mountain chain border (Irl et al., 2016; Leuschner, 1996). Such thermal advantages create favourable growing conditions for trees at higher elevations (Troll, 1973). Several studies argue that treelines at the same

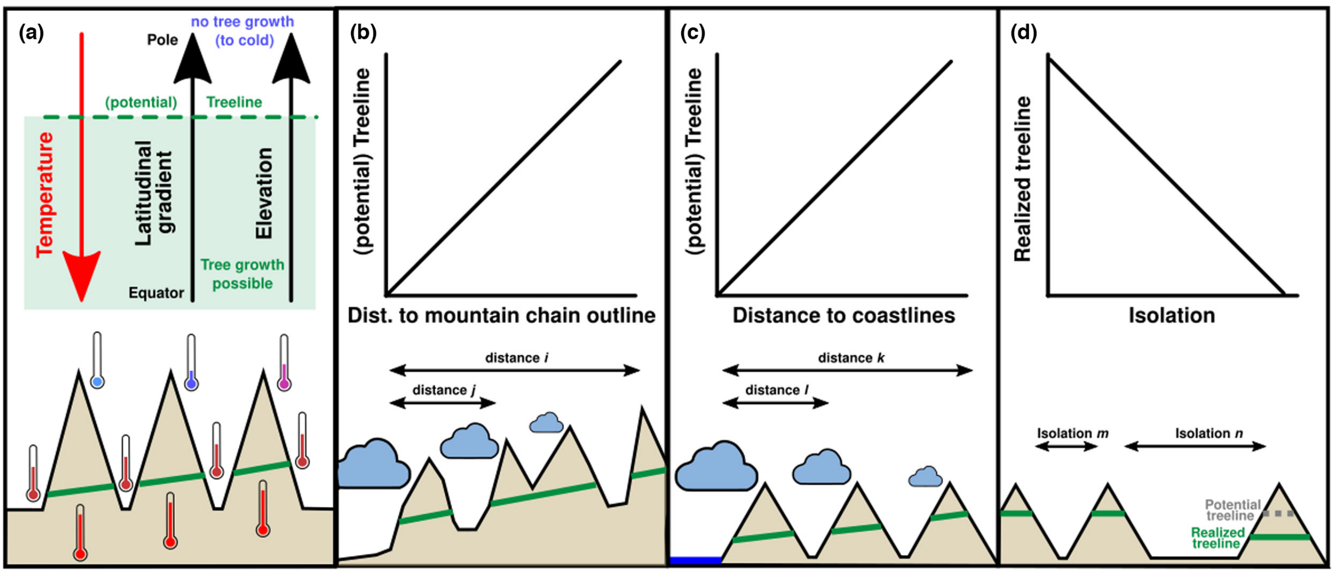


FIGURE 1 Indirect and direct drivers of treeline elevations. (a) An ideal treeline will act as an isotherm due to enabled growing conditions (Körner, 1998, 2007). Latitudes and elevation have an opposite trend to the temperature. (b) Mass elevation effect (MEE) reduces cloudiness with increasing distance from the mountain chain outlines. Consequently, growing temperatures increase with increasing distances from the mountain chain outline. (c) Cloudiness as an aspect of continentality decreases with increasing distance from the coastlines. Temperatures increase resulting in increasing distances from the coastlines. Mass elevation effect and distance to the coasts increase the potential treeline indirectly via increasing the temperatures. (d) The realized treeline decreases with increasing isolation which results in a realized treeline below of the potential treeline.

latitudes located in the centre of mountain chains occur at higher elevations than at its margins or on remote peaks (Ellenberg, 1963; Troll, 1973). However, approaches to quantify the MEE are scarce. Case and Duncan (2014) used the area above a given elevation as a proxy; however, elevation translates to different thermal conditions at regional scales. Han et al. (2010), Han et al. (2012) and Zhao et al. (2015) calculated a mountain base elevation for subregions of mountain chains, based on catchments of rivers. This approach avoids latitudinal dependencies but is computationally complex and involves an unclear causal relationship to the MEE. Based on the arguments given above, we propose to use the distance of a treeline location to the mountain chain border as a ready-to-use and easy-to-calculate measure of MEE.

Distance to the coastlines influences treeline elevations inside large landmasses due to a decrease in cloudiness resulting in an increase in growing temperatures. Thus, we interpret this distance as a proxy of one aspect of continental climate: low cloudiness. This leads to increased solar radiation and thus increasing thermoclines in more continental climates that result in ameliorated growing conditions for trees at high elevations, even if mountain chains cause adiabatic uplift and condensation of air humidity. Consequently, we assume treelines are higher in continental than in oceanic mountains. Evident limits exist in arid and hyperarid regions where non-forested ecosystems exist because conditions are too dry for tree growth. Continentality effects on treelines were documented in regional (Daubenmire, 1954; Griggs, 1934; Holtmeier, 2003) and global studies (Zhao et al., 2015).

Mountains exhibit different levels of isolation with consequences on biotic processes and the species pool, respectively (Flantua et al., 2020; MacArthur & Wilson, 1963; Steinbauer et al., 2016). Following Paulsen and Körner (2014), a temperature-controlled potential of tree growth exists that translates into a *potential treeline* for a respective latitude and elevation. Possible candidates to occupy ecological niches close to this potential treeline will be less likely to occur with increasing isolation, leading to the *realized treeline* being lower than the potential treeline (Figure 1d). This debt in niche saturation is characteristic for high mountains and becomes less relevant with decreasing elevation of treeline towards higher latitude. On isolated islands, the deviation from expectation becomes even stronger (Irl et al., 2016; Leuschner, 1996). The probability of occurrence of cold-adapted tree species decreases with isolation and smaller species pools as the ecological distance to the next comparable habitat is more pronounced than the distance to the next foothills (Steinbauer et al., 2016). The relevance of this has been shown in regional (Brockmann-Jerosch, 1919; Itow, 1992; Körner & Paulsen, 2004) and global studies (Irl et al., 2016; Karger et al., 2019). This fact might not only apply to oceanic islands. Isolated high mountains in a lowland matrix such as the East African volcanic peaks are examples of comparable isolation of the alpine zone. In these cases, it is likely that isolation also affects the treeline of highly isolated continental mountains as a result of dispersal filters to the environmental variables (Steinbauer et al., 2016).

Here, we aim to identify drivers of variation in the global latitude-treeline relationship with a high spatial resolution. We used minimum distance measures to the mountain chain outlines, coastlines and locations of the same elevation as proxies for MEE, distance to coastlines and isolation. We expect (i) MEE and (ii) distance to coastlines to increase treeline elevation, if latitude is accounted for, while (iii) isolation will decrease treeline elevation. We offer ready-to-use and reproducible measures of MEE and a cloud-relevant aspect of continentality: distances to coastline or mountain borders are independent of elevation and come at a low computational cost. Like recent studies (Irl et al., 2016; Paulsen & Körner, 2014), we systematically sample a global data set of treeline elevations based on free accessible Google Earth aerial images.

2 | MATERIALS AND METHODS

2.1 | Treeline data

Treeline data were sampled with the software Google Earth, which allows a consistent, systematic global analysis of remote sensing and aerial images combined with an underlying digital elevation model (SRTM 90 × 90 m resolution). This software provides the possibility to detect single tree individuals and was already used in two previous studies in treeline research studies (Irl et al., 2016; Paulsen & Körner, 2014). In this study, the observed realized treeline was defined as a roughly connected line of the highest tree patches in the surrounding area. This definition of the treeline is consistent with several studies (Hermes, 1955; Irl et al., 2016; Karger et al., 2019; Körner, 2012; Paulsen & Körner, 2014).

When sampling treeline presences and absences we used a three-step approach to determine a representative data set. We considered all elevations, including highly isolated mountaintops and islands. Firstly, we randomly selected 30 search locations per elevational layer of 200 m height between −200 m and 5400 m a.s.l. in increments of 100 m. Secondly, we put search locations along a global isolation gradient based on our isolation data. For each 10th quantile along this gradient, 30 random search locations were investigated. Thirdly, we included island data ($n = 96$) from Irl et al. (2016). We excluded data points in this step if they appeared less than 12 km to samples already obtained in steps 1 and 2 to avoid any duplications. This approach yielded a data set covering the complete spectrum of potential elevations and biomes. The data set applied in this study includes 629 locations with a treeline and 1051 without a treeline (Figure 2; Kienle et al., 2023).

We scaled Google Earth's GUI interface to a buffer size of approximately 6000 m from a perspective of 100 m (±20 m) above Earth's surface. Within this buffer zone, we took coordinates and elevation of the highest treeline locations. In some remote areas of Russia and Canada, individual trees were not identifiable due to insufficient image resolution. If this was the case, no treeline was sampled, unless we detected another visible treeline within the 6000 m buffer and took this next highest treeline.

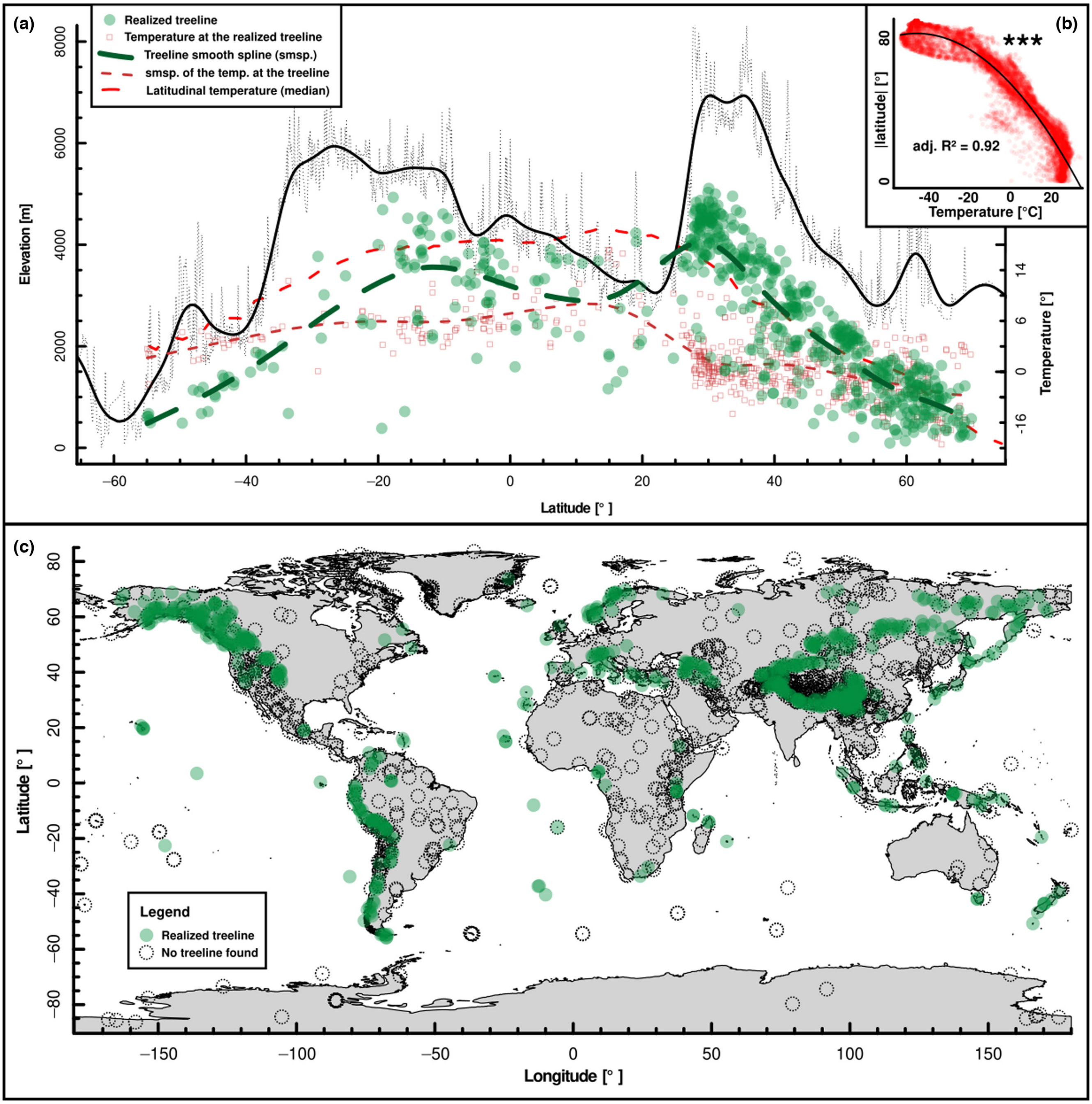


FIGURE 2 Global distribution of realized alpine treelines. (a) Treeline elevations (green dots) show a double hump-shaped pattern with latitudes (green long-dashed smooth spline, spar = 1). The latitudinal terrestrial temperature (median of annual mean temperatures, red continuous line) follows roughly the treeline smooth spline whereas the temperature at the realized treeline (red rectangles) shows a more linear and flatter pattern (red short-dashed smooth spline, spar = 1). Black lines show the latitudinal maximum elevation based on a digital elevation model (DEM; small-dotted line based on 1 km × 1 km cell sizes, continues line smooth spline, spar = 0.5). (b) Global mean temperature (10.000 randomly selected terrestrial points) correlates with absolute values of latitudes. (c) Map showing sampling locations. All elevations below 5400 m a.s.l. and remote areas (oceanic islands) are included. In total, 672 treeline presences (green dots) and 1051 treeline absences (unfilled dots, no clear treeline detectable) below or above the treeline had been detected.

2.2 | Quantification of mass elevation effect, continentality and isolation

Quantitative analyses of the MEE require a definition of the borders (outlines) of mountain chains. Körner et al. (2011) introduced the approach using a given ruggedness as the definition of mountainous areas. Ruggedness is independent of elevation itself and therefore excludes large plateaus. The MEE of a treeline sample was measured as the nearest distance to the mountain chain border of Körner et al. (2011)'s mountain classification.

We used the shortest distance to the coastline as an aspect of continentality. We excluded twelve sites on islands because it was not possible to measure distances as a result of imprecisely georeferenced aerial images.

We quantified isolation for each pixel of the world by distances to the closest areas of the same elevation based on a digital elevation model. We used SRTM cells of 12 × 12 km to provide a helpful trade-off between computing power and the dispersal ecology of tree species. We used elevational bands of 100 m and calculated distances inside these bands. Therefore, we considered the curvature of the Earth but ignored the nearest distances crossing the poles since we assume them as prominent barriers for species migrations. In the rare case of steep slopes, different nearest distances were associated with the same raster cell. If so, we averaged distances to consider gradual changes in nature. As a result, we assigned an isolation value to each treeline location.

2.3 | Global temperature data

To relate geographic drivers and analysis with climatic variables, we included global temperature data from the CHELSA data set (Karger et al., 2017). We extracted annual air temperature values (bio1) based on three different approaches: (a) for the comparison with the latitudes we selected 10,000 random points on the land masses (b) to get the median of the temperature for each latitude we selected again 10,000 random points per latitude and (c) for the temperature of the treeline we selected values based on the coordinates of our treeline samples.

2.4 | Statistical analysis

Global latitudinal trends of treeline, maximum land surface elevations, and the variables mean temperature, distance to the mountain chain outline, distance to the coastline and isolation were fitted with a smooth spline to the data. We tested the effect of temperature on treeline elevation using linear and 2-polinomial regression models. Furthermore, we tested the relationship between temperature and absolute values of latitudes. Assumed relationships between the different variables were tested with structural equation models based on the function *psem* from the R package *piecewiseSEM* (Lefcheck, 2020). To test our hypotheses, we first applied a unimodal regression on the latitude-treeline relationship following the assumption that this is the most prominent global relationship. Subsequently, we tested the effects of MEE, distance to coastlines and isolation using the residuals of this model. For all three explanatory variables, the best model fit was a logarithmic regression. Second, we calculated partitioned variances for the three variables MEE, distance to coastlines and isolation with the function *varpart* from the R package *vegan* to identify the joint and independent explained variance for each explanatory variable (Oksanen et al., 2020). All analyses were done in R Statistics (R Core Team, 2021).

3 | RESULTS

We observed a bimodal pattern of treelines and latitudes (Figure 2a). Southern and Northern hemisphere treelines decreased significantly with increasing latitudes. Global treeline elevations were best explained with a unimodal regression (F (2, 628) = 618.8; $p < 0.0001$; adj. R^2: 0.66; latitude^2: slope = −1.04488 ± 0.03304; latitude: slope = 17.11344 ± 1.56413). Even when treelines on islands were ignored, a tropical depression was still visible. Between about 7° and 29°N very few treelines occurred. However, a tropical depression between 15°S and 7°N is still visible. The mentioned treeline gap between 7° and 29°N coincides with the comparable low elevation global landmasses at these latitudes. The treeline gap north of the equatorial tropics is also visible in the geographic distribution of the treeline samples (Figures 2c and 5b–d).

Comparing 10.000 randomly selected terrestrial points showed clearly that temperature and absolute values of latitudes correlate with each other (Figure 2b; F (2, 9997) = 56.490; $p < 0.0001$; adj. R^2: 0.92; temp^2: slope = −0.0133641 ± 0.0001397; temp: slope = −1.218 8171 ± 0.0040003), resulting in the median curve of temperatures along latitudes (Figure 2a). In contrast, temperature directly at the treeline location has only a small effect on the treeline elevation, but the best explanatory model fit lacks a suitable fit to the scatterplot (Figure 3a; F (2, 628) = 31.86; $p < 0.0001$; adj. R^2: 0.09; temp^2: slope = −6.2133 ± 0.8188; temp: slope = 40.7492 ± 8.4142).

Treeline elevation increased linearly in log-space with increasing treeline distance to mountain chain borders (Figure 3b; F (1, 629) = 419.0; $p < 0.000$; adj. $R^2 = 0.40$; log10(distance): slope = 1043.32 ± 50.97). Treeline elevation increased linearly in log-space with increasing distance to the coastline (Figure 3c; F (1, 626) = 335.1; $p < 0.0001$; adj. $R^2 = 0.35$; log10(distance): slope = 554.12 ± 30.27). With increasing isolation, treeline elevations decreased (Figure 3d; F (1, 629) = 105.0; $p < 0.0001$; adj. $R^2 = 0.14$; log10(isolation): slope = −309.83 ± 30.24). Isolation affected treeline elevation only in subtropical regions (but not in the equatorial tropics; Figure 5a).

We applied a structural equation model to further examine the relationships of the various variables to each other and on the treeline elevation. Distance to the mountain chain outline, distance to the coastline and temperature had strong effects on the treeline elevation, isolation a small effect (Figure 4a). Distance to the mountain chain outline and distance to the coastline had effects on each other and on temperature.

The variance partitioning revealed that within mountain chains the explained variance was highest for MEE (0.40), followed by distance to coastlines (0.27). Isolation only played a very subordinate role (0.14). MEE and distance to coastlines shared a large overlap of joint explained variance (Figure 4b). Outside of mountain chains distance to coastlines explained the most variance, jointly and independently. Again, isolation only was of subordinate importance. As well the distances to the mountain chain outline as to the coastline explain large amounts of variance, whereas isolation accounts for a smaller amount. There are large parts of shared explaining variance.

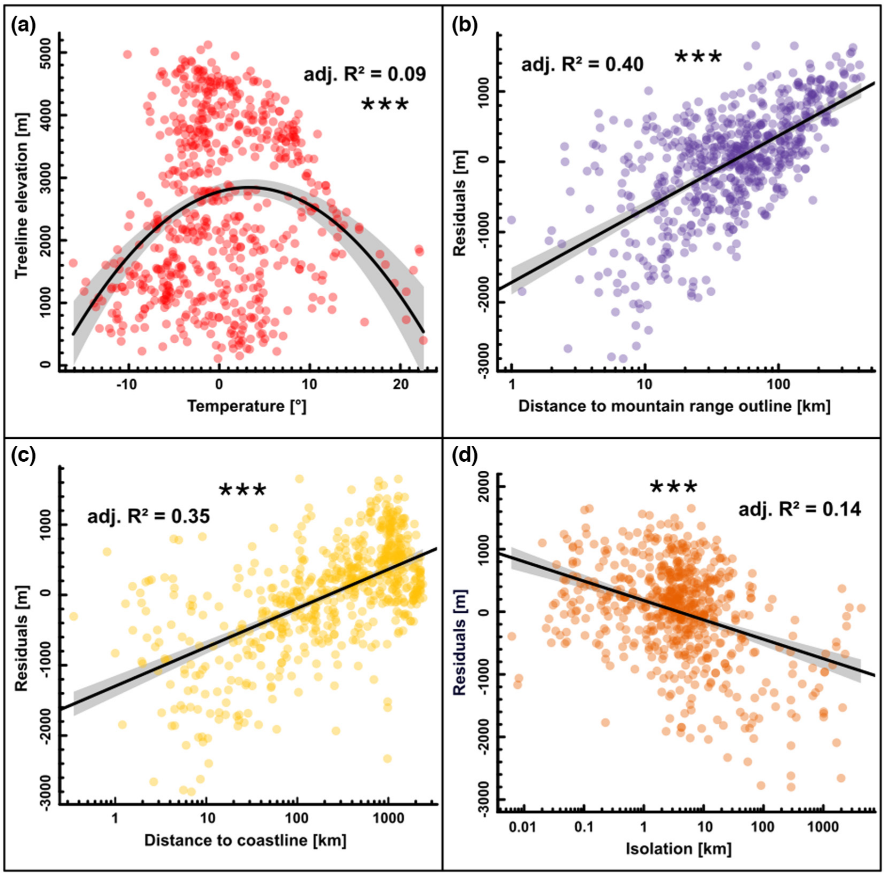


FIGURE 3 Effects of temperature, distance to mountain chain outline (mass elevation effect), distance to coastlines and isolation. Note that all distances are log-scaled and some regressions are based on the residuals of the quadratic regression which explained treeline elevations with latitudes (c–d). Asterisks indicate significance (***$p < 0.001$). (a) Treeline elevation explained by the temperature found at the treeline. The best explanatory model was a 2-polinomial regression model. (b) Treeline elevations explained by mass elevation effect (measured with the distance to mountain chain borders). Treeline elevation increased with increasing distance to mountain chain borders. (c) Treeline elevation explained by distance to the coastlines. Treeline elevations increased with increasing distance from coastlines. (d) Treeline elevations explained by isolation. Treeline elevation decreases with increasing isolation.

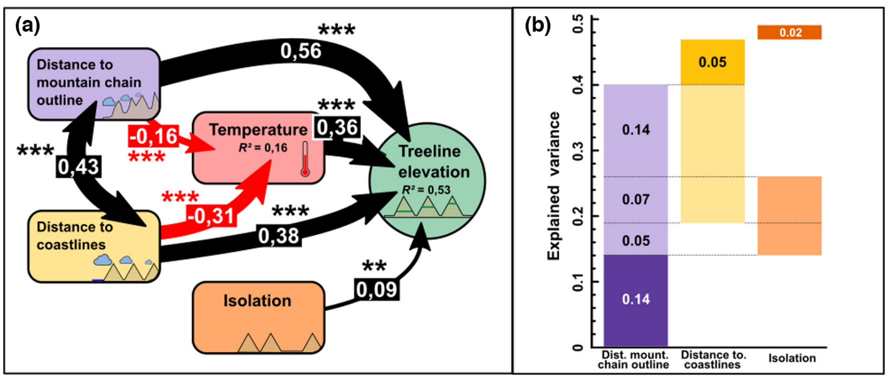
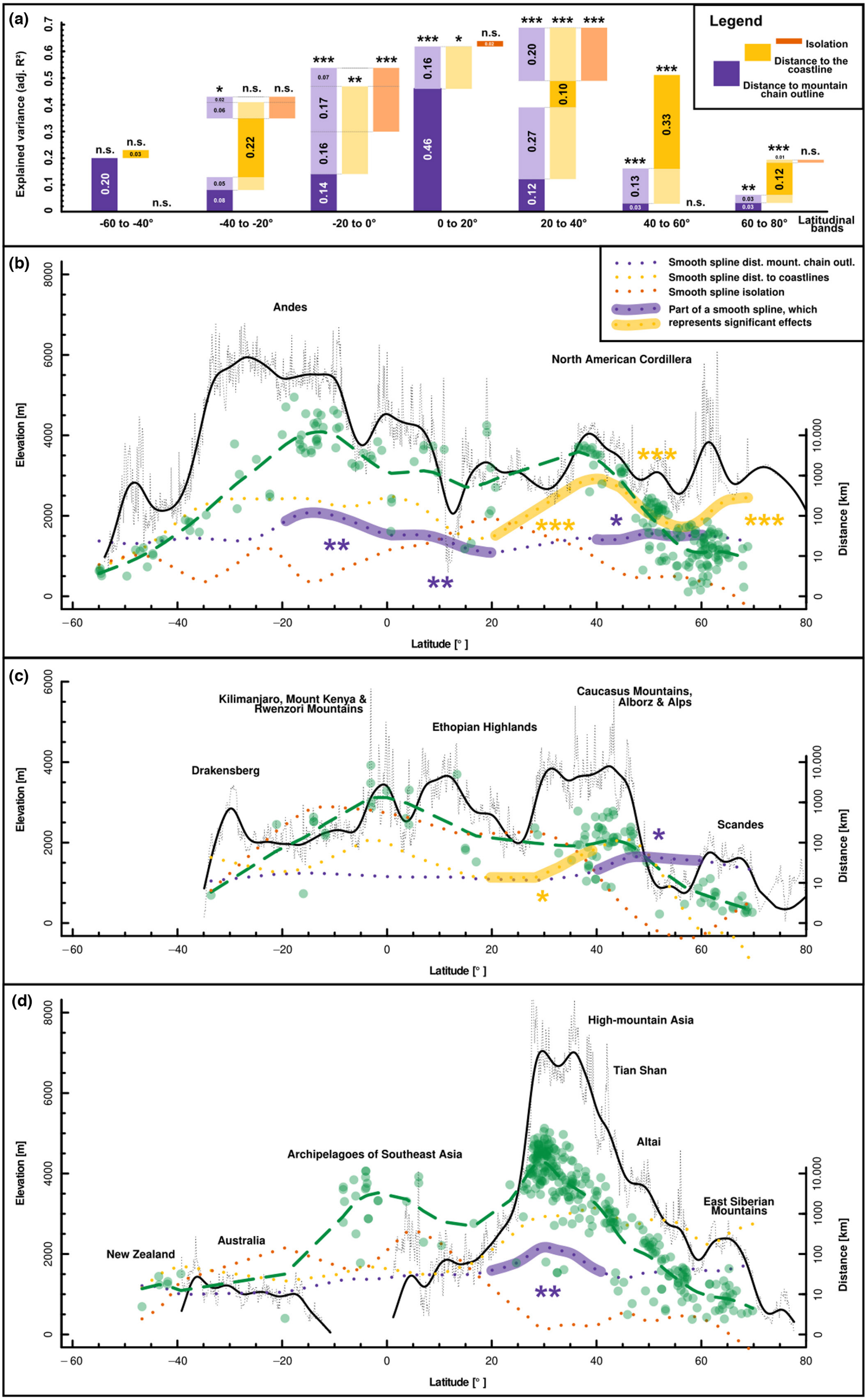


FIGURE 4 (a) Relationships of the different variables based on a structural equation model (standardized values used for all variables). MEE, distance to the coastline and temperature had a strong positive effect on treeline elevation. In addition, a strong negative effect of distance to the coastline on temperature was also found, whereas the effect of MEE on temperature and that of isolation on treeline elevation were rather small. (b) Variance partitioning between the variables distance to the mountain chain outline, distance to coastlines and isolation.

FIGURE 5 Detailed illustration of the latitudinal distribution of the treeline elevation and the studied variables. (a) Variance partitioning between the variables distance to the mountain chain outline, distance to coastlines and isolation for different latitudinal bands. Asterisks indicate significances (***$p < 0.001$) of the underlying linear models of the respective variables limited to latitudinal bands. (b–d) Latitudinal distribution of treeline elevations for different longitudinal regions. Treeline elevations (green dots) show a slight double hump-shaped pattern on all continents; however, the trend is recognizable based on the existing land masses and high mountains (green long-dashed smooth spline, spar = 1). Dotted pink, yellow and orange smooth splines indicate the latitudinal mean of the distances to mountain mass outline, coastline and isolation (smooth spline, spar = 1). They were transparently highlighted if a segmented linear regression of the corresponding latitudinal band contained significant correlations. Black lines show the latitudinal continental maximum elevation based on a digital elevation model (DEM; small-dotted line based on 1 km × 1 km cell sizes, continues line smooth spline, spar = 0.5). (b) Treelines at longitudes up to −30°; (c) Treelines with longitudes from −30° and up to 60°; (d) Treelines above longitudes of 60°.


(a)
Explained variance (adj. R²)
Legend
Isolation
Distance to the coastline
Distance to mountain chain outline
-60 to -40°
-40 to -20°
-20 to 0°
0 to 20°
20 to 40°
40 to 60°
60 to 80°
Latitudinal bands
(b)
Smooth spline dist. mount. chain outl.
Smooth spline dist. to coastlines
Smooth spline isolation
Part of a smooth spline, which represents significant effects
Andes
North American Cordillera
Elevation [m]
Distance [km]
Latitude [°]
(c)
Kilimanjaro, Mount Kenya & Rwenzori Mountains
Caucasus Mountains, Alborz & Alps
Ethopian Highlands
Drakensberg
Scandes
Elevation [m]
Distance [km]
Latitude [°]
(d)
High-mountain Asia
Tian Shan
Altai
Archipelagoes of Southeast Asia
East Siberian Mountains
Australia
New Zealand
Elevation [m]
Distance [km]
Latitude [°]

Isolation only includes shared variances; the other two variables incorporate also non-shared parts of variance.

Effects of the distance to the mountain chain outline, distance to the coastline and isolation differed greatly along latitudes and in different mountain systems on different continents (Figure 5). The distance to the coastline had a large effect especially in North America, whereas the distance to the mountain chain outline played a large role especially in the Andes and in High Mountain Asia. We found largest isolations in the tropics and isolation had an opposite trend to the distribution of land masses on the continents but has no significant independent explanatory components.

4 | DISCUSSION

Our study adds to our understanding of how global patterns of treeline formation in mountainous regions are modulated by spatial characteristics of mountain chains on the regional scale. In our comprehensive global treeline study, we identify two key regional sources of variation in the global bimodal latitude-treeline relationship—MEE and continentality. As hypothesized, both MEE and continentality have a positive effect on treeline elevation, likely by ameliorating thermal growing conditions at high elevations via reduced atmospheric absorption of solar radiation by clouds, air moisture or aerosols. Interestingly, the third driver proposed in this study—isolation-driven differences in the species pool of (potential) treeline species—plays only a minor role.

4.1 | Global latitude-treeline relationship

We find a bimodal relationship between latitude and global treeline elevations, symmetric around a thermal equator at about 7°N. Our results, showing a subtropical double hump, fit to recent empirical studies (Irl et al., 2016; Karger et al., 2019; Zhao et al., 2015) and bioclimatic predictions (Paulsen & Körner, 2014).

These findings confirm classic biogeographic studies such as Troll (1948) and Ellenberg (1963) indicating treelines and related vegetational patterns to be lower in the equatorial tropics than in the subtropics due to diurnal climate leading to reoccurring night frost. However, it could also be an artefact of lacking high continental mountains in the equatorial tropics between 0° and 29° North because large mountain chains are missing here. Furthermore, these latitudes contain a high degree of island treelines that tend to be lower than on continents (Irl et al., 2016; Karger et al., 2019; Leuschner, 1996).

4.2 | Mass elevation effect

Treeline elevation increases with increasing distances to mountain borders. This is consistent with theoretical consideration of the MEE (Ellenberg, 1966; Körner, 2012; Schröter, 1908), and our study can robustly quantify this effect. In consequence, MEE improves plant growth and in particular, tree growth at high elevations on a global scale. Although there are different concepts in quantifying MEE (Case & Duncan, 2014; Han et al., 2010; Holtmeier, 2003; Pouteau et al., 2018; Zhao et al., 2015), all authors argue that MEE increases treeline elevations via improved growing conditions through an increased solar radiation. Our results indicate that MEE modulates treelines globally, from small islands to large mountain chains. The smaller the mountain chain (or island) is, the lower the treeline. The effect is stronger in large mountain chains, resulting in a comparably high treeline.

For highly arid areas, a Merriam effect has been described (Richter, 1996): precipitation and cloudiness increase towards the centre of mountain chains following moist adiabatic processes by rising air fluxes. This Merriam effect will only play a role for treelines in areas with very low precipitation since some tree species can tolerate conditions with very low precipitation (Miehe et al., 2007). However, such an effect was not supported by our results. In general, the MEE is active across different scales from small entities such as islands (Irl et al., 2016; Karger et al., 2019; Pouteau et al., 2018) through the continental scale (Han et al., 2010, 2012) to the global scale (Zhao et al., 2015; and this study).

4.3 | Continentality

Continental climate has a prominent influence on the arrangement of biomes and the treeline, representing one of the most prominent boundaries between them. Our results show clearly that treeline elevations increase with increasing continentality measured as distance to the coastline. Also, a part of the variance inside of mountain chains is explained by this distance alone. Both results indicate that the continental climate of large landmasses increases treeline elevations independent of mountain chains. This is in accordance with other studies (Jobbágy & Jackson, 2000; Zhao et al., 2015). In fact, it fits well to the observed lower treelines in the Southern Hemisphere compared with the Northern Hemisphere (Jobbágy & Jackson, 2000). This is likely a result of generally smaller Southern Hemisphere landmasses with less continental heating and more oceanic climate (Cieraad et al., 2014; Körner, 1998).

A combination of extreme continentality-related low cloudiness and high MEE explains the fact that the world's highest treelines are found in the interior of large subtropical mountain chains in very continental regions, for example in the Central Andes (Hoch & Körner, 2005) and in Tibet (Miehe et al., 2007). In contrast, oceanic islands generally exhibit lower treelines than mainland mountains that are comparable in latitude and size (Irl et al., 2016; Karger et al., 2019).

4.4 | Isolation

Treeline elevation decreases with increasing spatial isolation. However, the independent effect of isolation on treeline elevation was quite minor and could not be statistically separated from the effect of continentality. This is likely the case because, on the global scale, the most isolated mountains are islands that have very oceanic climates (Karger et al., 2019) and thus, per definition, a low degree of continentality. Nevertheless, the effect of isolation on the species pool of (potential) treeline species is well documented, especially for islands (Irl et al., 2016; Karger et al., 2019; Leuschner, 1996). Consequently, we argue that isolation is relevant, albeit only to a small degree, for treeline elevations on a global scale.

Nevertheless, there is often a gap even on continents between the potential thermal treeline and the actual formation of a treeline as a result of biogeographic influences. In other words, a potential treeline may not necessarily be realized because the observable treeline lies below the maximal thermal treeline of a certain area. Isolation emphasizes the physically independent effect of random events, which merely depend on space and time.

A highly isolated, not yet realized potential treeline will only emerge as a result of two possibilities: (i) if a treeline species, suitable to the extreme local conditions, immigrates from somewhere else. This considers—in an adaptation of island biogeography theory (MacArthur & Wilson, 1963)—that this species can overcome the surrounding matrix of lower elevations. Since the matrix of lower elevations (with more suitable growing conditions) contains a high amount of highly competitive tree species (Ghalambor et al., 2006), a direct vector may be needed. In this case, stochastic events (e.g., species migration, random dispersal events) play an increasing role with increasing distances. This is supported by our results since the variance of treeline elevations increased with increasing isolation. (ii) A potential treeline species evolves in situ, occupying the empty niche of a treeline species and leading to the realization of the thermal treeline potential. Furthermore, time will play a more prominent role in the evolution of a well-adapted treeline species. Our findings illustrate that isolation effects were stronger on islands compared to continents and, especially highly isolated oceanic islands are often geological quite young, likely resulting in an impoverishment of tree species pool regarding high elevation tree species (Leuschner, 1996).

Not only did an increase of isolation increase the variance of treeline elevation—the variance even increased the more a treeline site was located towards the tropics. This might depend on the large number of treelines that are located on islands in tropical regions and are therefore more isolated than treelines on continents. For instance, the Indo-Malayan Archipelago contains many more treeline samples than the African and American continent in comparable (tropical) latitudes. Even Africa's equatorial treelines are highly isolated from each other resulting in isolated volcanic peaks (e.g., Kilimanjaro, Rwenzori, Mt. Kenya, Mt. Cameroon). The equatorial tropics in general lack large and high mountain chains (except for the Andes) which has been discussed to be a result of a comparably exceptionally strong climate-driven erosion process (Egholm et al., 2009). Consequently, it can be assumed that mountains in the tropics, particularly in the equatorial tropics, are often not high enough to reach the potential treeline.

5 | CONCLUSION

Our results show a clear, globally measurable MEE. Both, MEE and continentality increase treeline elevation with increasing distances. MEE and continentality reduce cloud cover and increase solar radiation and temperature, resulting in higher treeline elevations. Isolation is a measurable, but a minor driver of treeline elevation on the global scale. Although island biogeographic theory suggests an effect of isolation, it appears to play a major role in treeline elevations only on islands. Our study of geographic drivers of treeline contributes to better understand how environmental conditions determine the limits of life forms on large spatial scales. This will become even more important with global warming and a potentially more pronounced cloudiness gradient with more extreme climates.

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CONFLICT OF INTEREST STATEMENT

All co-authors confirm that they have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The used data fall under no licence (CC0 1.0 Universal) and are free available in Dryad: https://doi.org/doi:10.5061/dryad.7h44j0zzk. Furthermore, the data are available in this git repository: https://codeberg.org/IsolEcol/global-treelines.

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BIOSKETCHES

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