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LETTER

Are treelines advancing? A global meta-analysis of treeline response to climate warming

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Abstract

Treelines are temperature sensitive transition zones that are expected to respond to climate warming by advancing beyond their current position. Response to climate warming over the last century, however, has been mixed, with some treelines showing evidence of recruitment at higher altitudes and/or latitudes (advance) whereas others reveal no marked change in the upper limit of tree establishment. To explore this variation, we analysed a global dataset of 166 sites for which treeline dynamics had been recorded since 1900 AD. Advance was recorded at 52% of sites with only 1% reporting treeline recession. Treelines that experienced strong winter warming were more likely to have advanced, and treelines with a diffuse form were more likely to have advanced than those with an abrupt or krummholz form. Diffuse treelines may be more responsive to warming because they are more strongly growth limited, whereas other treeline forms may be subject to additional constraints.

Keywords

Abrupt, advance, climate change, diffuse, forest dynamics, global meta-analysis, krummholz, temperature, treeline.

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INTRODUCTION

Average temperatures have risen globally over the past century, with the most pronounced and rapid changes at high altitudes and latitudes (Solomon *et al.* 2007). Within these zones, treeline position is widely thought to be temperature sensitive and potentially responsive to climate warming (Kupfer & Cairns 1996; Holtmeier & Broll 2005). For this reason, the dynamics of the upper altitudinal or latitudinal tree limit have been studied around the globe with the aim of detecting change, understanding responses to temperature variation, and evaluating the threat to alpine and arctic biota in response to treeline movement in high altitude and latitude communities (Foley *et al.* 1994; Holtmeier & Broll 2007).

Temperature is widely considered to be the primary control on treeline formation and maintenance (Mikola 1962; Körner 2007). Supporting evidence includes global relationships between treeline position and temperature isotherms (Grace 1977; Körner & Paulsen 2004), fluctuations in treeline position in accordance with past temperature changes (Grace 1989; Foley *et al.* 1994; Lloyd & Graumlich 1997), and recent recruitment beyond historical treeline limits consistent with observed rates of recent warming (Suarez *et al.* 1999; Gamache & Payette 2005; Truong *et al.* 2006; Shiyatov *et al.* 2007). In particular, the prevailing view is that high altitude and latitude treelines are controlled by summer temperatures (Holtmeier & Broll 2007; Gehrig-Fasel *et al.* 2008; MacDonald *et al.* 2008), with treeline position over much of the globe coinciding with a mean growing season temperature of 5–6 °C (Körner & Paulsen 2004). This implies that treelines should be particularly responsive to changes in summer temperature, although other studies suggest that the effects of winter temperature on survival may also play a role (Kullman 2007; Rickebusch *et al.* 2007).

Although treelines are considered thermally limited and average temperatures have increased globally over the last century, treeline advance is not a worldwide phenomenon (Holtmeier & Broll 2007). This disjunction between rising average temperatures and expected treeline response could be due to spatially non-uniform patterns of temperature change. There can be marked variation in the degree to which local sites or regions have warmed or even cooled on average over the last century (Lindkvist & Lindqvist 1997; Körner 2007), along with differences in the extent to which sites have experienced summer or winter warming (Armbruster *et al.* 2007). Variation in treeline response may reflect this local spatial variability in average and seasonal temperature changes, rather than mean global trends.

In addition, temperature may not be the dominant factor controlling treeline position at some sites. This is because the direct influence of temperature may be masked by interactions with other factors such as precipitation (Daniels & Veblen 2003; Wang *et al.* 2006), cold-induced photoinhibition (Danby & Hik 2007), disturbance (Lescop-Sinclair & Payette 1995; Cullen *et al.* 2001) or plant–plant interactions (Germino *et al.* 2002; Bekker 2005). Furthermore, tree responses may be asynchronous with the rate of warming, either lagging behind or occurring only after a threshold level of warming has occurred (Rupp *et al.* 2001).

The considerable variability in topography and local climates associated with treelines worldwide, and their differing taxonomic composition, undoubtedly complicates the picture and limits the conclusions that can be drawn from single studies. On the other hand, global overviews that ignore local differences may overemphasize coarse-scale drivers such as temperature (e.g. Körner & Paulsen 2004). To avoid the limitations of both these approaches, we compiled a global dataset of individual treeline studies in relation to local and regional environmental variables with the aim of comparing changes in treeline position over the last century.

In this study we determine the global extent to which treelines have advanced, specifically testing the hypothesis that the probability of treeline advance since 1900 AD is linked to the degree of local temperature warming, and explore the possibility that factors other than temperature may influence treeline response to climate warming.

MATERIAL AND METHODS

Database

Treeline studies published prior to June 2008 were identified using journal search tools (Web of Science, BIOSIS, JSTOR, Proquest Dissertations and Theses search), internet web searches and by direct communication with the authors of studies. To reduce error associated with publication bias, whereby reports of treeline advance were expected to be published more often than reports of no advance, we used a general search criterion to identify studies that may not have set out to document treeline changes, but where appropriate methods to detect changes were used.

Treelines are conventionally defined as the upper altitudinal or latitudinal limit in which upright trees reach either two or three metres in height, but may also be defined by the presence of krummholz trees. As the definition of a treeline varies considerably among studies, we included only those studies in which the authors explicitly stated that the study area included the upper tree (at least 2 m in height) or krummholz limit. Studies in which the uppermost tree height was > 3 m were included only if it was noted that no other trees or krummholz existed beyond the treeline. Treelines were classed as having advanced or not since 1900 AD according to explicit statements in each study regarding the nature of treeline movement. Treeline advance was not limited to changes in trees 2 m or more in height but included seedlings and saplings. In comparing those studies in which the authors classed treelines as having advanced, vs. those that had not, treeline advance was reported if there was evidence of recruitment since 1900 AD at least 10 m beyond the historic position of alpine treelines, and at least 80 m beyond the historic position of latitudinal treelines. Where authors reported the size of trees used to infer advance (159 of 166 studies), 53% reported new recruits > 2 m tall (i.e. a clear shift in treeline position) while the remainder of studies inferred advance from recent recruitment of trees that had not yet reached 2 m in height. Although some studies reported advance prior to 1900 AD, our analyses were limited to responses observed after this date. Changes in density below current treeline, or a change in growth form from krummholz to upright were not classed as evidence of treeline advance. Studies were omitted where no data on recruitment beyond the current upper tree limit or krummholz belt was reported. Treelines reported as receding (2/166) were included but classed as not advancing. Data quality limited the response to a binary variable 'advance or not' since quantitative estimates of the rate of change were not reported consistently.

We examined 243 treeline studies, for which treeline advance or not since 1900 AD could be classified for 103. These 103 studies reported responses from 166 treeline sites (36 studies included data from multiple sites), comprising 126 alpine and 40 latitudinal treelines from around the world, but with most sites in North America or Europe (Fig. 1). Of the 36 studies reporting data from multiple sites, 25 reported the same response at all sites examined. The studies had used three general approaches to assess treeline response: long-term monitoring of permanent plots (43 sites), remote sensing, mostly aerial photographs (27 sites) and treeline/stand history reconstruction using growth rings to age trees and date establishment (96 sites).

To determine whether treeline advance was related to recent temperature changes, we used a dataset of global historical land surface temperatures (GHCN; Peterson & Vose 1997) comprising monthly temperature data from *c.* 7000 stations around the world. We removed duplicate station records and retained only stations with at least 50 years of complete monthly data since 1900 AD (2651 stations). For each of the 166 treeline sites, we identified the nearest climate station (using great circle distance) and

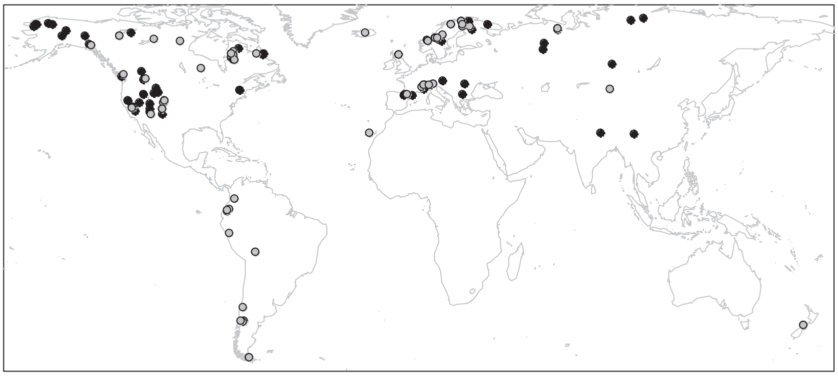

Figure 1 The location of the 166 treeline sites across the globe analysed in this study grouped according to whether they are advancing (black circles) or not advancing (grey circles).

downloaded the historical mean monthly temperature data for that station. We calculated mean annual temperature as the average of the mean monthly temperatures for each year. The annual rate of change in temperature over the duration of the study, defined by study start and end dates, was estimated as the slope of the least squares regression line for the relationship between mean annual temperature and year for the period 10 years prior to the start of the study through to when the study finished. End date refers to the final year observations were made and start date refers to either the first year of observations (e.g. repeat photography, long-term monitoring) or the first year after 1900 AD in which trees were dated in stand history reconstructions. We included temperature data for 10 years prior to the start of the study because treeline change may lag behind temperature change, and at some sites there was evidence of advance prior to the start of the study. When the study start date preceded 1900 AD (i.e. prior to the onset of recent human-induced warming), we calculated change in annual temperature from 1900 AD to when the study finished. We also calculated rate of temperature change for the summer months (June–August in the Northern hemisphere and December–February in the Southern hemisphere) and winter months (December–February in the Northern hemisphere and June–August in the Southern hemisphere).

For each site, we collated additional explanatory variables that are routinely reported as proxies for exposure to environmental stress (reviewed in Smith *et al.* 2003): treeline form, elevation, latitude, distance from the ocean, aspect and treeline type. We also included variables that could affect our ability to detect a response: study duration, study start date, study scale and disturbance (Table 1; Appendix 1), along with the taxonomic family of the treeline species, because treeline position and potentially response have been identified as having a taxonomic component (Körner & Paulsen 2004).

Elevation, latitude, aspect and treeline type were obtained from information in the published studies. Aspect was classed as warm (south facing in the Northern hemisphere and north facing in the Southern hemisphere), cold (north facing in the Northern hemisphere and south facing in the Southern hemisphere) or neutral (east and west facing). Treeline type was classed as alpine or latitudinal. Distance to the ocean was calculated as the distance from the study site to the nearest coastline using ArcView 9.1 (ArcGIS Version 9.1; Computer Software, ESRI Redlands, CA, USA).

Treeline form refers to the spatial structure of the treeline at the start of the study. We recognized three treeline forms: (1) diffuse – characterized by decreasing tree density with increasing altitude or latitude; (2) abrupt – a continuous canopy with no decline in density right up to treeline; and (3) krummholz – the treeline may be diffuse or abrupt but is characterized by severely stunted or deformed polycormic trees. Tree height often declines with elevation or latitude in both diffuse and abrupt treelines but was not considered indicative of these forms. When more than one treeline form was recorded at a study site, we used the form recorded at the uppermost altitudinal or latitudinal treeline limit. In the case where both krummholz and upright trees occur at the upper limit, the treeline was classed as krummholz. Treeline form was inferred primarily from written descriptions and, when necessary, photographs or direct communication with authors.

Evidence for disturbance at each site was classed as: unknown (no information on disturbance recorded), none (an explicit statement that there was no evidence of disturbance at the site), natural (e.g. evidence of wind, natural fire and earthquake) or anthropogenic (e.g. evidence of agriculture, livestock grazing and fire suppression). We did not record data on the timing or intensity of disturbance because this was reported inconsistently. We used study methodology as a proxy for the effect of scale on our ability to detect treeline advance. In general, field based studies (long-term monitoring and stand history reconstructions) were at a finer scale and smaller spatial extent than those relying on remote sensing (repeat photography and satellite imagery) methods.

Table 1 Definition and sample size of variables used in model formulation

Variable	Class	No. sites	Range
Aspect	Warm	30	
	Cold	36	
	Neutral	67	
Distance from ocean		166	13.8–2883 km (539 km)
Disturbance	None	110	
	Natural	16	
	Anthropogenic	33	
Elevation		155	4–4330 m a.s.l. (1560 m a.s.l.)
Family		166	
Form	Abrupt	10	
	Diffuse	82	
	Krummholz	69	
Latitude		166	−54.13 to 70.52° (51.44°)
Annual temperature change		166	−0.026 to 0.049 °C $year^{-1}$ (0.006 °C $year^{-1}$)
Summer temperature change		166	−0.038 to 0.09 °C $year^{-1}$ (0.011 °C $year^{-1}$)
Winter temperature change		166	−0.044 to 0.084 °C $year^{-1}$ (−0.002 °C $year^{-1}$)
Study duration		166	1–108 years (63 years)
Study start date		166	1900–2006
Study Scale	Coarse	27	
	Fine	139	
Treeline type	Alpine	126	
	Latitudinal	40	

The range (minimum–maximum) and mean (in parentheses) of continuous variables are shown.

Analysis

We used logistic regression models to determine whether treeline advance or not was associated with the explanatory variables. We fitted these models in a Bayesian framework so that we could accommodate plant family as a random effect in the model, and to deal with missing values (Gelman & Hill 2007). Our dataset had 56 missing values for explanatory variables: aspect (33), elevation (11), disturbance (7) and treeline form (5), mostly where information was not available from published sources. Rather than omitting sites with missing values, which is the conventional approach assuming missing values occur at random (Gelman & Hill 2007), we modelled missing values for continuous variables as if they were drawn at random from a normal distribution having mean and variance estimated from the data, and missing values for categorical variables as if they were drawn from a multinomial distribution with the probability for each category estimated from the data (Gelman & Hill 2007). This allowed us to include all of the relevant data in the model while incorporating the uncertainty associated with estimating those missing values.

Our response variable was whether treeline advance had occurred since 1900 AD or not. We modelled this as a Bernoulli process with a logit link function, including rate of temperature change (annual and seasonal), treeline form, distance from ocean (log transformed), elevation (log transformed), latitude, study duration, study start date, aspect, disturbance, study scale (field observation *vs.* remote sensing) and treeline type as explanatory variables. The continuous explanatory variables (rate of annual and seasonal temperature change, distance from ocean, elevation, study duration and latitude) were standardized by subtracting their mean and dividing by twice their standard deviation to assist with model convergence and to put the parameter estimates for both continuous and categorical variables on a comparable scale (Gelman & Hill 2007). Categorical variables (treeline form, aspect, disturbance, study scale and treeline type) were included by coding them as dummy variables and choosing one of the classes as a reference class with the coefficient set to zero. Plant family was included as a random effect, with the regression coefficients describing the effect of each family assumed to be drawn from a common normal distribution with a mean of zero and a standard deviation estimated from the data.

Data on rate of temperature change were taken from the GHCN climate station closest to each treeline site, but the site-station distances varied from < 1 to 626 km (median = 77 km). To assess the significance of this, we investigated how differences among GHCN stations in their rate of temperature change varied as a function of both distance apart and difference in elevation (Appendix 2). Temperature trends differed among stations but there was no strong tendency for stations located further apart or those having a greater difference in elevation to differ systematically from stations located closer together or at similar elevation. Thus, while using temperature trends from climate stations located close to, but not at, treeline sites may introduce noise to our data, it should not generate any systematic bias.

We first included each explanatory variable alone in a logistic regression model to identify the variables with the greatest influence on treeline response. We then included in a multivariate model the subset of variables that tended to differ from zero in the logistic regression models, to asses their relationship with treeline advance having accounted for the effect of other variables. Plant family was also included as a random effect in the multivariate model to account for the possibility that species in the same plant family showed similar responses. Several studies included more than one site, which might result in correlated responses, but we did not include a study-level effect in the model because most studies (67 of 103) comprised only a single site.

The model was fitted using OpenBugs called from the BRugs library (Thomas *et al.* 2006) in R v. 2.8 (R Development Core Team 2008). We used non-informative prior distributions to reflect a lack of prior information about the model parameters, specifying a normal prior with variance 1000 for regression coefficients and a uniform prior in the interval 0–10 for variance parameters. We ran three chains each with a burn-in of 5000 iterations, which was sufficient to ensure convergence as judged by inspection of the chain histories, and then sampled the posterior distributions from a further 10 000 iterations of each chain. The importance of explanatory variables was assessed using 95% Bayesian credibility intervals on these posterior distributions.

RESULTS

Mean annual temperature increased at 111 of the 166 sites at an average rate of 0.013 °C year^{-1} over the study duration, although the rate of temperature increase was < 0.01 °C year^{-1} at over half of the sites experiencing warming (Fig. 2a). Summer warming occurred more often (117/166 or 71% of sites, mean = 0.0189 °C year^{-1}), than winter warming (77/166 or 46% of sites, mean = 0.0199 °C year^{-1}; Fig. 2).

Treelines had advanced since 1900 AD at 87 of 166 sites (52%) Figure 1. Of the sites that showed no advance, 77 had remained stable whereas two had receded, with the two sites where treelines had receded also showing evidence of disturbance. There was no clear association between probability of treeline advance and rate of mean annual or summer temperature increase. For example, of the 111 sites in which annual temperature had increased over the study

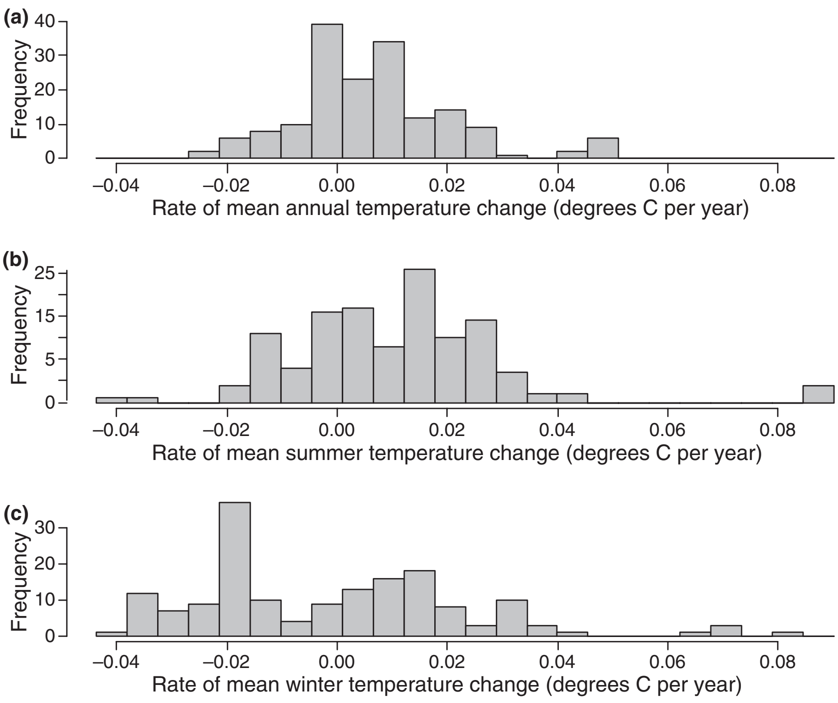

Figure 2 Histogram of the rate of (a) annual, (b) summer and (c) winter temperature change (°C year^{-1}) for the 166 study sites for the period 10 years prior to study start date to the study finish date.

duration, 63 (57%) had advanced, and of the 55 sites that had cooled, 24 (44%) had advanced. Indeed the 95% credible intervals for the parameter estimates describing the relationship between the probability of treeline advance and rate of annual and summer temperature change, when these were included alone in a model, overlapped zero (Fig. 3a). In contrast, treelines were more likely to advance at sites that had warmed during the winter months: the parameter estimate for the relationship between probability of treeline advance and rate of winter temperature change, when included alone, was positive and 95% credible intervals did not include zero (Fig. 3a).

Disturbance, study duration, study start date, latitude, aspect, treeline type and scale did not show strong relationships with probability of treeline advance when each variable was included alone in a logistic regression model (the 95% credibility intervals around the parameter estimates all overlapped zero; Fig. 3a,b). In contrast, the parameter estimates for rate of winter temperature change, elevation, distance to ocean and treeline form tended to differ from zero. We therefore fitted a multivariate model that included these four explanatory variables along with plant family as a random effect.

Having accounted for the effects of the other variables in the model, elevation and distance to ocean failed to show a clear relationship with probability of advance (Fig. 3c). Rate of winter temperature change was associated with probability of advance, with 95% credible intervals excluding zero: sites that had warmed more during the winter months were more likely to have advanced. The strongest relationship was with treeline form: diffuse treelines were more likely to have advanced than krummholz and abrupt treelines (Fig. 3c). Of the 82 treeline sites classed as diffuse, 67 (80%) had advanced, whereas of the 79 sites classed as abrupt or krummholz only 17 (22%) had advanced (five sites were unclassified with regards to treeline form).

There were no clear differences among plant families in their probability of advance having accounted for other variables in the model (Fig. 4). This may reflect the strong bias towards species in the Pinaceae and Betulaceae, which formed the treeline at 136 sites (82%). Species in other families occurred at few sites, limiting our ability to detect differences.

Finally, to explore the relationship between temperature change and treeline form further, we modelled the relationship between rate of mean annual, summer and winter temperature change and probability of advance, separately for diffuse treelines and for abrupt and krummholz treelines combined (Fig. 5). There is evidence that treelines with differing form have different temperature responses. Diffuse treelines were more likely to advance

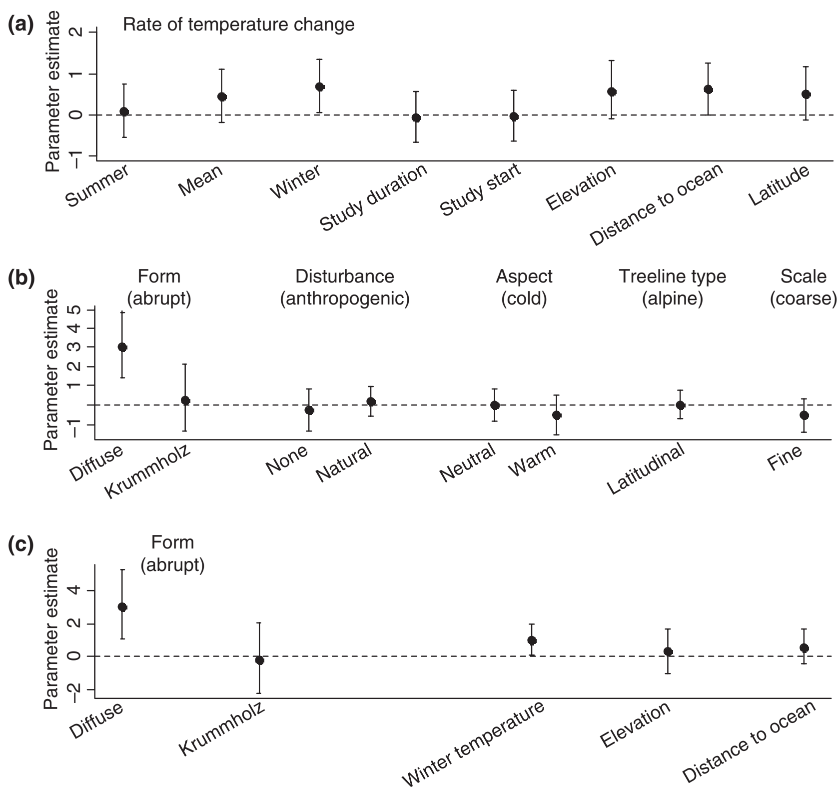

Figure 3 The mean and 95% credible intervals for the parameter estimates describing the effect of each explanatory variable on the probability of treeline advance when those variables are included alone in a logistic regression model (a, b) or together in a multivariate logistic regression model with plant family included as a random effect (c). The continuous variables (rate of temperature change, distance from ocean, elevation, study duration and latitude) were standardized by subtracting their mean and dividing by two times their standard deviation. The parameter estimates for the levels of the factor variables are with regard to a reference class (shown in parentheses), which is set to zero. Credible intervals crossing the zero line (dashed) are not significant.

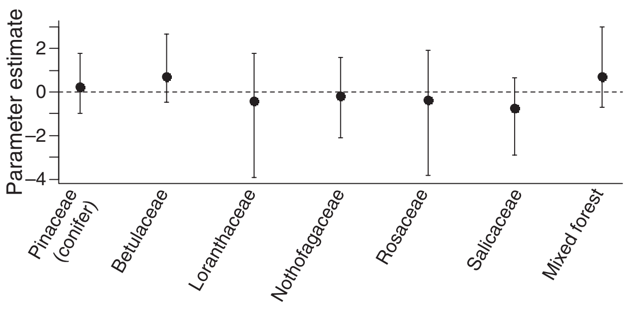

Figure 4 The mean and 95% credible intervals for the parameter estimates describing the effect of plant family on the probability of treeline advance. Conifer treelines comprise only the family Pinaceae, while all other families are angiosperms. Mixed forests are treeline sites composed of both gymnosperm and angiosperm families. Credible intervals crossing the zero line (dashed) are not significant.

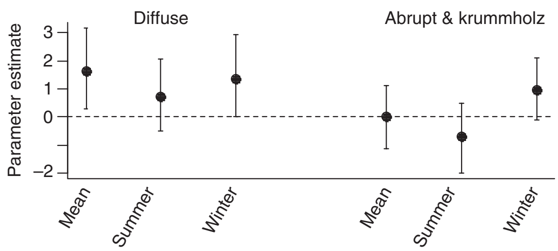

Figure 5 The mean and 95% credible intervals for the parameter estimates describing the effect of rate of mean annual, summer and winter temperature change on probability of treeline advance, for diffuse and abrupt and krummholz treelines separately. Credible intervals crossing the zero line (dashed) are not significant.

when warming occurred (mean annual, summer or winter), having the strongest association with mean annual and winter warming. In contrast, abrupt and krummholz treelines were more likely to advance only with winter warming.

DISCUSSION

Our global analysis indicates that, regardless of form, location and degree of temperature change experienced over the last century, treeline positions have either advanced or remained stable. At only two sites were treelines recorded as receding and both of these sites showed evidence of disturbance. This is consistent with what might be expected if treelines were responding to increasing global temperature but were also constrained by other factors. In contrast, we would expect to observe no advance or random fluctuations around a zero trend line (approximately equal numbers of advances and retreats) in the absence of directional change. Unless receding treelines have been systematically under-reported, the net global outcome is that treelines are rising. Advance, however, was not universal.

Of the variables we considered, two were strongly associated with treeline response: treelines that experienced stronger winter warming were more likely to advance, and treelines with a diffuse form were more likely to advance than treelines with abrupt or krummholz forms. At a global scale, treelines are considered to be constrained primarily by growing season temperature (Körner & Paulsen 2004). That treeline advance is more strongly associated with winter, rather than summer, warming is therefore surprising. The observed relationship with winter warming alone was apparent only for abrupt and krummholz treelines; diffuse treelines appear to be responding to overall increases in temperature (Fig. 5). This variation in the response of treeline forms to seasonal and annual temperature change may result from different primary constraints on treeline position; diffuse treelines, in contrast to abrupt and krummholz treelines, are more likely to form where climatic factors, particulary growing season temperature, primarily limit growth rather than survival (Camarero & Gutierrez 2002; Danby & Hik 2007). Although there is a body of evidence suggesting that diffuse treelines are limited by growing season temperature (Ellenberg 1988; Wiegand *et al.* 2006), our results do not provide such evidence but do suggest that diffuse treelines are responding to overall warming, of which summer warming is a component (Fig. 5).

In contrast, abrupt or krummholz treelines may be more strongly influenced by stress factors associated with winter conditions that lead to plant damage and limit survival. Krummholz form, in particular, is commonly attributed to damage associated with factors such as wind abrasion, snow and ice damage (Norton & Schoenberger 1984; Hadley & Smith 1986) which can be severe during late autumn, winter and early spring. Considering that recruitment by seed is infrequent during unfavourable periods (Laberge *et al.* 2001; Caccianiga & Payette 2006) and that tall seedling growth is likely limited by the same factors that limit vertical growth in krummholz (Smith *et al.* 2003), recruitment beyond the krummholz belt is unlikely to occur unless conditions limiting vertical growth are lessened. Likewise, the step-like structure of abrupt treelines can arise because harsh winter conditions limit survival in open sites due to factors such as winter desiccation (Cairns 2001). These factors may be ameliorated by the presence of tall, closed canopy trees leading to an abrupt boundary at treeline. Such feedback effects in turn may constrain the response of these treelines to climate warming (Bader *et al.* 2007). Hence, advance in krummholz and abrupt treelines may occur only when winter warming is sufficient to ameliorate other constraints, or when temperatures increase sufficiently to compensate for those constraints.

Although treelines with higher rates of winter warming were more likely to show advance, there was much variability around this relationship, with many sites classed as advancing even when mean winter temperature over the study duration had cooled. Several reasons are frequently proposed to explain why treelines fail to respond to temperature changes as expected. First, study methodology could have a pronounced effect on ability to detect change. The inclusion of remotely sensed (coarse-scale) methodologies may decrease our ability to detect a response because they may be less effective at detecting small shifts in altitude or latitude. However, there was no significant difference between coarse- and fine-scale studies in their ability to detect advance (Fig. 3b).

Second, ecological time lags (e.g. slow-growing species, rare seeding events) may delay recruitment. Treeline advance has been shown to lag behind climate warming at some sites, but typically by only a few decades (Lescop-Sinclair & Payette 1995; Kullman 2001; Lloyd *et al.* 2003). Most of our studies began well after the onset of 20th century warming, or were of sufficient duration to exceed these lag periods. Disturbance legacies may further influence treeline position and its ability to respond to climate changes. Past disturbances can shape treeline structure and influence initial recruitment patterns but subsequent patterns of recruitment and spread may be more strongly controlled by climate (Holtmeier & Broll 2005; Bolli *et al.* 2007; Vittoz *et al.* 2008). Hence, rather than affecting the probability of recent advance, disturbance may influence when advance initiates and act as a potential lag source. We found no evidence in our data of different responses at sites that varied in known disturbance history, suggesting any long-lasting effects of disturbance cannot explain the patterns observed in this study.

Finally, interannual variation can have a significant affect on treeline advance. Recruitment and survival are both highly sensitive to short periods markedly cooler or warmer than the general temperature trend (Kitzberger *et al.* 2000; Gray *et al.* 2006). For example, recruitment observed at a site with a cooling trend may have occurred during a brief warm period, and recruitment at a site with a warming trend may have been hindered by a short cold period that killed new recruits. Until the general warming trend consistently exceeds interannual variability, treeline advance may depend upon the coincidence of favourable conditions over sufficient years to permit establishment, growth and survival (Szeicz & MacDonald 1995; Wang *et al.* 2006). This is less likely to be critical for diffuse treelines if summer growth limits treeline position, because growth gains in warmer summers are likely to be retained through cooler summers. In contrast, where treeline advance is limited by winter survival, a single cold year could destroy the gains made over several warmer winters.

In summary, approximately half the treeline sites examined globally have advanced since 1900 AD, with a link between probability of advance and the degree of local winter warming at those sites. These results are consistent with what we would expect if treelines were responding to increasing global temperatures but were also constrained by other factors. In particular, diffuse treelines are more likely to advance than abrupt or krummholz treelines. We speculate that diffuse treelines may be strongly limited by growing season temperatures and hence particularly responsive to overall temperature increases. Abrupt and krummholz treelines, in contrast, may be more strongly limited by winter temperatures in association with other constraints that act on tree survival, such as damage due to wind, snow or winter desiccation. Advance at these sites may require an increase in winter temperature sufficient to ameliorate the impact of these other constraints.

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REFERENCES

Armbruster, S.W., Rae, D.A. & Edwards, M.E. (2007). Topographic complexity and terrestrial biotic response to high-latitude climate change: Variance is as important as the mean. In: *Arctic Alpine Ecosystems and People in a Changing Environment* (eds. Ørbæk, J.B., Kallenborn, R., Tombre, I., Hegseth, E.N., Falk-Petersen, S. & Hoel, A.H.). Springer Berlin, pp. 105–121.

Bader, M.Y., van Geloof, I. & Rietkerk, M. (2007). High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecol.*, 191, 33–45.

Bekker, M.F. (2005). Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. *Arct. Antarct. Alp. Res.*, 37, 97–107.

Bolli, J.C., Rigling, A. & Bugmann, H. (2007). The influence of changes in climate and land-use on regeneration dynamics of Norway spruce at the treeline in the Swiss Alps. *Silva. Fenn.*, 41, 55–70.

Caccianiga, M. & Payette, S. (2006). Recent advance of White spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Quebec, Canada). *J. Biogeogr.*, 33, 2120–2135.

Cairns, D.M. (2001). Patterns of winter desiccation in krummholz forms of abies lasiocarpa at treeline sites in Glacier National Park, Montana, USA. *Geogr. Ann.*, 83A, 157–168.

Camarero, J.J. & Gutierrez, E. (2002). Plant species distribution across two contrasting treeline ecotones in the Spanish Pyrenees. *Plant Ecol.*, 162, 247–257.

Cullen, L.E., Stewart, G.H., Duncan, R.P. & Palmer, J.G. (2001). Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *J. Ecol.*, 89, 1061–1071.

Danby, R.K. & Hik, D.S. (2007). Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Glob. Chang. Biol.*, 13, 437–451.

Daniels, L.D. & Veblen, T.T. (2003). Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *J. Veg. Sci.*, 14, 733–742.

Ellenberg, H. (1988). *Vegetation Ecology of Central Europe*, 4th edn. Cambridge University Press, Cambridge.

Foley, J.A., Kutzbach, J.E., Coe, M.T. & Levis, S. (1994). Feedbacks between climate and boreal forests during the Holocene epoch. *Nature*, 371, 52–54.

Gamache, I. & Payette, S. (2005). Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. *J. Biogeogr.*, 32, 849–862.

Gehrig-Fasel, J., Guisan, A. & Zimmerman, N.E. (2008). Evaluating thermal treeline indicators based on air and soil temperature using an air-to-soil temperature transfer model. *Ecol. Model.*, 213, 345–355.

Gelman, A. & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/*Hierarchical Models. Cambridge University Press, New York.

Germino, M.J., Smith, W.K. & Resor, A.C. (2002). Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecol.*, 162, 157–168.

Grace, J. (1977). *Plant Responses to Wind*. Academic Press, London.

Grace, J. (1989). Tree lines. *Philos. Trans. R. Soc. Lond.*, 324, 233–245.

Gray, S.T., Betancourt, J.L., Jackson, S.T. & Eddy, R.G. (2006). Role of multidecadal climate variability in a range extension of Pinyon pine. *Ecology*, 87, 1124–1130.

Hadley, J.L. & Smith, W.K. (1986). Wind effects on needles of timberline conifers – seasonal influence on mortality. *Ecology*, 67, 12–19.

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

Holtmeier, F. & Broll, G. (2007). Treeline advance-driving processes and adverse factors. *Landsc. Online*, 1, 1–33.

Kitzberger, T., Steinaker, D.F. & Veblen, T.T. (2000). Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, 81, 1914–1924.

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends Ecol. Evol.*, 22, 569–574.

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

Kullman, L. (2001). 20th century climate warming and the tree-limit rise in the Southern Scandes of Sweden. *Ambio*, 30, 72–80.

Kullman, L. (2007). Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973-2005: implications for tree line theory and climate change ecology. *J. Ecology*, 95, 41–52.

Kupfer, J.A. & Cairns, D.M. (1996). The suitability of montane ecotones as indicators of global climatic change. *Prog. Phys. Geogr.*, 20, 253–272.

Laberge, M.J., Payette, S. & Pitre, N. (2001). Development of stunted black spruce (*Picea mariana*) clones in the subarctic environment: a dendro-architectural analysis. *Ecoscience*, 8, 489–498.

Lescop-Sinclair, K. & Payette, S. (1995). Recent advance of the arctic treeline along the eastern coast of Hudson Bay. *J. Ecol.*, 83, 929–936.

Lindkvist, L. & Lindqvist, S. (1997). Spatial and temporal variability of nocturnal summer frost in elevated complex terrain. *Agric. For. Meteorol.*, 87, 139–153.

Lloyd, A.H. & Graumlich, L.J. (1997). Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*, 78, 1199–1210.

Lloyd, A.H., Rupp, T.S., Fastie, C.L. & Starfield, A.M. (2003). Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. *J. Geophys. Res.*, 108, 2–1.

MacDonald, G.M., Kremenetski, K.V. & Beilman, D.W. (2008). Climate change and the northern Russian treeline zone. *Philos. Trans. R. Soc. B*, 363, 2285–2299.

Mikola, P. (1962). Temperature and tree growth near the northern timberline. In: *Tree Growth* (ed. Kozlowski, T.T.). Rondal Press, New York, pp. 265–274.

Norton, D.A. & Schoenberger, W. (1984). The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. *Arctic Alpine Res.*, 16, 361–370.

Peterson, T.C. & Vose, R.S. (1997). An overview of the global historical climatology network temperature database. *Bulletin of the American Meteorological Society*, 78, 2837–2849.

R Development Core Team (2008). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Rickebusch, S., Lischke, H., Bugmann, H., Guisan, A. & Zimmermann, N.E. (2007). Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. *For. Ecol. Manage.*, 246, 251–263.

Rupp, T.S., Chapin, F.S. III & Starfield, A.M. (2001). Modeling the influence of topographic barriers on treeline at the forest-tundra ecotone in Northwestern Alaska. *Clim. Change*, 48, 399–416.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. (eds.) (2007). *Climate change 2007: The physical science basis*. Cambridge University Press, Cambridge.

Shiyatov, S.G., Terent'ev, M.M., Fomin, V.V. & Zimmermann, N.E. (2007). Altitudinal and horizontal shifts of the upper boundaries of open and closed forests in the Polar Urals in the 20th century. *Russ. J. Ecol.*, 38, 223–227.

Smith, W.K., Germino, M.J., Hancock, T.E. & Johnson, D.M. (2003). Another perspective on altitudinal limits of alpine timberlines. *Tree Physiol.*, 23, 1101–1112.

Suarez, F., Binkley, D. & Kaye, M.W. (1999). Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska. *Ecoscience*, 6, 465–470.

Szeicz, J.M. & MacDonald, G.M. (1995). Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *J. Ecol.*, 83, 873–885.

Thomas, A., O'Hara, B., Ligges, U. & Sturtz, S. (2006). Making BUGS Open. *R News*, 6, 12–17.

Truong, C., Palme, A.E. & Felber, F. (2006). Recent invasion of the mountain birch *Betula pubescens* spp *tortuosa* above the treeline due to climate change: genetic and ecological study in northern Sweden. *J. Evol. Biol.*, 20, 369–380.

Vittoz, P., Rulence, B., Largey, T. & Frelechoux, F. (2008). Effects of climate and land-use change on the establishment and growth of Cembran pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the Central Swiss Alps. *Arct. Antarct. Alp. Res.*, 40, 225–232.

Wang, T., Zhang, Q. & Ma, K. (2006). Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. *Glob. Ecol. Biogeogr.*, 15, 406–415.

Wiegand, T., Camarero, J.J., Ruger, N. & Gutierrez, E. (2006). Abrupt population changes in treeline ecotones along smooth gradients. *J. Ecol.*, 94, 880–892.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Database used for analysis.

Appendix S2 Assessment of how differences among GHCN stations in the rate of temperature change varied as a function of distance a part and differences in elevation.

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