



Is subarctic forest advance able to keep pace with climate change?

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Abstract

Recent climate warming and scenarios for further warming have led to expectations of rapid movement of ecological boundaries. Here we focus on the circumarctic forest–tundra ecotone (FTE), which represents an important bioclimatic zone with feedbacks from forest advance and corresponding tundra disappearance (up to 50% loss predicted this century) driving widespread ecological and climatic changes. We address FTE advance and climate history relations over the 20th century, using FTE response data from 151 sites across the circumarctic area and site-specific climate data. Specifically, we investigate spatial uniformity of FTE advance, statistical associations with 20th century climate trends, and whether advance rates match climate change velocities (CCVs). Study sites diverged into four regions (Eastern Canada; Central and Western Canada and Alaska; Siberia; and Western Eurasia) based on their climate history, although all were characterized by similar qualitative patterns of behaviour (with about half of the sites showing advancing behaviour). The main associations between climate trend variables and behaviour indicate the importance of precipitation rather than temperature for both qualitative and quantitative behaviours, and the importance of non-growing season as well as growing season months. Poleward latitudinal advance rates differed significantly among regions, being smallest in Eastern Canada (~10 m/year) and largest in Western Eurasia (~100 m/year). These rates were 1–2 orders of magnitude smaller than expected if vegetation distribution remained in equilibrium with climate. The many biotic and abiotic factors influencing FTE behaviour make poleward advance rates matching predicted 21st century CCVs (~10³–10⁴ m/year) unlikely. The lack of empirical evidence for swift forest relocation and the discrepancy between CCV and FTE response contradict equilibrium model-based assumptions and warrant caution when assessing global-change-related biotic and abiotic implications, including land–atmosphere feedbacks and carbon sequestration.

W. Gareth Rees and Annika Hofgaard should be considered joint first author of this paper.

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circumpolar forest advance, climate change, climate change velocity, disappearing arctic tundra, forest migration rate, forest–tundra ecotone, range expansion, subarctic

1 | INTRODUCTION

Biomes and the transition zones between them are expected to shift under the influence of climate change because of species' range shifts (Parmesan & Yohe, 2003; Settele et al., 2014). Range adaptation to altering climate conditions has been an ongoing process throughout the Holocene (Davis & Shaw, 2001; Williams, Shuman, Webb III, Bartlein, & Leduc, 2004), but the rate of climate change is commonly expected to accelerate during the present century (Collins et al., 2013; Settele et al., 2014). The individual responses of species to changing climate, in aggregate, result in reorganization of species assemblages and shifts in biome boundaries. It thus follows that contemporary climate change should result in shifts of major biomes across the globe. Such shifts, however, may be more varied than simple uniform poleward displacement (Lenoir & Svenning, 2015; Merlin, Duputié, & Chuine, 2018). In this paper, we consider specifically the transition zone between the boreal forest and the arctic tundra at regional and circumarctic levels. This zone, the forest–tundra ecotone (henceforward FTE), is Earth's areally most extensive ecological boundary (Callaghan et al., 2002) and is expected to undergo substantial climate-mediated change during the present century (Larsen et al., 2014). Changes in its extent or location would have profound bioclimatic implications well beyond the region (ACIA, 2005; Alley et al., 2007; Kaplan & New, 2006; Solomon et al., 2007; van Bogaert et al., 2011), including associated climate-related feedbacks (Chapin III et al., 2005; de Wit et al., 2014; Pearson et al., 2013).

Qualitative field observations (i.e. describing the movement status of the boundary) representing recent decades have generally revealed biomes shifting to higher latitudes and upslope (Dufour-Tremblay, Levesque, & Boudreau, 2012; Elsen & Tingley, 2015; Gonzalez, Neilson, Lenihan, & Drapek, 2010; Hofgaard, Tømmervik, Rees, & Hanssen, 2013; Savage & Vellend, 2014), although opposite latitudinal shifts are also reported (Carpino, Berg, Quinton, & Adams, 2018; Payette, 2007; Timoney et al., 2018; Vlassova, 2002). Projections of future range shifts have until lately been dominated by Ecological Niche Models (ENMs; otherwise species distribution models or climate envelope models) and their predecessors, based on correlations between existing environmental factors and species distributions (Loehle, 2018; Peterson et al., 2011) and thus assuming equilibrium between climate and vegetation. Inevitably, the approach implies that vegetation distributions should more or less keep pace with climate change. The concept of climate change velocity (CCV; Loarie et al., 2009) is especially relevant to such equilibrium models, indicating the rate at which an organism would need to move to keep pace with the changing climate (Burrows et al., 2011; Chen, Hill,

Ohlemüller, Roy, & Thomas, 2011). CCVs vary spatially and may be different for different aspects of climate (e.g. temperature and precipitation, and their month-specific CCVs). Future CCVs also depend on the assumed climate change scenario, but typical values are of order 10^3 – 10^4 m/year over the 21st century (Settele et al., 2014). These values underpin predictions by ENMs of northward forest advances of up to 7,000–20,000 m/year and upslope shifts of 2–6 m/year, and consequently huge (11%–50%) displacement of arctic tundra by boreal forest (Callaghan et al., 2005; Pearson et al., 2013). Use of process-based models, in recent years, as prediction tools of future species ranges (Beale & Lennon, 2012; Cheaib et al., 2012; Morin & Thuiller, 2009; Settele et al., 2014) generally predicts smaller shifts than ENMs. However even so, they only consider a limited number of important change-related factors, and maximum advance rates remain uncertain (Cheddadi et al., 2014; Feurdean et al., 2013).

Neither ENMs nor process-based models are currently able to incorporate the range of abiotic and biotic factors associated with FTE advance (Dyderski, Paž, Frelich, & Jagodziński, 2017; Settele et al., 2014). Although experiments designed to analyse the role of the main ecological or site-specific factors governing boundary response provide valuable knowledge about the short-term significance of some FTE drivers (Lett & Dorrepaal, 2018; Løkken, Hofgaard, Dalen, & Hytteborn, 2019; Olofsson et al., 2009; Speed, Austrheim, Hester, & Mysterud, 2010), responses to climate change depend on a multitude of abiotic and biotic factors whose effective roles are highly variable through time and space (Hofgaard et al., 2013; Holtmeier & Broll, 2005; Martin, Jeffers, Petrokofsky, Myers-Smith, & Macias-Fauria, 2017). Behaviours and rates based on driver-restricted short-term data could thus be of limited value if used in long-term models (Callaghan et al., 2002; Harsch, Hulme, McGlone, & Duncan, 2009; Hofgaard et al., 2013; Kullman & Öberg, 2009). Observed FTE changes have been associated with driving factors such as climate warming (Macias-Fauria, Forbes, Zetterberg, & Kumpula, 2012; Tape, Sturm, & Racine, 2006; Walker et al., 2012), sea ice decline (Bhatt et al., 2010), permafrost thaw (Christensen et al., 2004), productivity change (Forbes, Macias Fauria, & Zetterberg, 2010), wild-fire (Payette, Fortin, & Gamache, 2001), direct human influences (Tømmervik, Bjerke, Park, Hanssen, & Myneni, 2019), and herbivory (Cairns & Moen, 2004; Olofsson et al., 2009). In addition, all include several possible intra-factor feedback mechanisms complicating understanding of resulting qualitative and quantitative (i.e. describing the rate of change of position) FTE behaviours.

Although there is an increasingly prevalent view that equilibrium models are unrealistic in their prediction of the rate at which terrestrial biomes will shift in response to changing climate (Settele et al., 2014), there is a shortage of quantitative data with which to

refine more sophisticated process-based models. To assess the realism of current models of the behaviour of the circumarctic FTE, and to guide the development of more accurate models, an extensive circumarctic survey of recent quantitative FTE behaviour is needed. While the existing literature indicates that encroachment of forest into tundra globally is not occurring in a spatially uniform manner (Harsch et al., 2009; Mamet, Brown, Trant, & Laroque, 2019), a systematic assessment of quantitative advance rates has so far been lacking. Satellite remote sensing methods offer the potential of temporally and spatially consistent datasets over very wide areas (Callaghan et al., 2002; Rees, Brown, Mikkola, Virtanen, & Werkman, 2002), and have produced important information on shifting tundra vegetation (Jia, Epstein, & Walker, 2003; Phoenix & Bjerke, 2016; Xu et al., 2013). However, despite the development of satellite data products designed specifically to show the distribution of woody vegetation (DeFries, Hansen, & Townshend, 2000; Garcia Criado, Myers-Smith, Bjorkman, Lehmann, & Stevens, 2020; Hansen et al., 2003, 2013; Sexton et al., 2013), deriving a reliable FTE product from them is not straightforward (Chopping, 2012; Montesano et al., 2009, 2014; Ranson, Montesano, & Nelson, 2011), and they do not extend far enough back in time to form the basis of a reliable understanding of FTE behaviour in the 20th century.

In the present paper, we address the question of advance of the circumarctic FTE over the 20th century by the use of data on its behaviour assembled from a large number of sites distributed around the circumarctic region. Specifically, we investigate whether

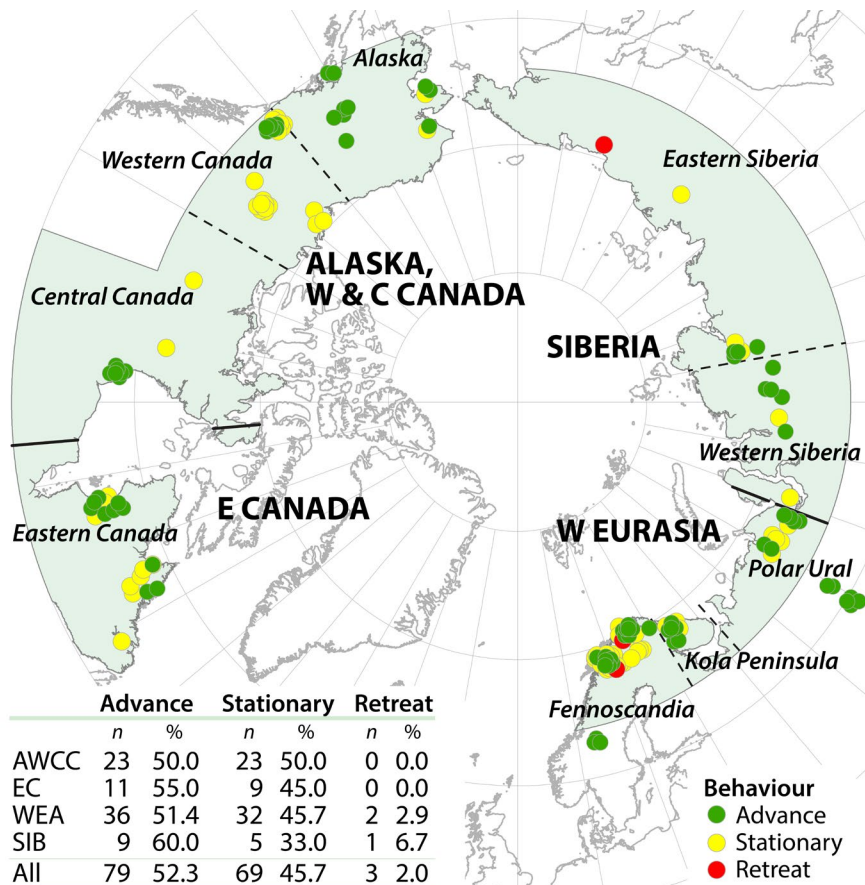
the phenomenon of FTE advance is uniformly distributed in the circumarctic region, and whether the presence or absence of advancing behaviour and advance rates are related to 20th century climate history. Furthermore, we consider whether rates of advance are consistent with typical CCV values and discuss the implications of climate history associations for the behaviour of the FTE in the 21st century in light of projected climate change.

2 | MATERIALS AND METHODS

2.1 | Data collection

The assembled data (Data S1) include published and unpublished FTE movement data representing 151 sites from around the circumpolar north (Figure 1). In the data selection process, the FTE was defined to cover the transition zone from the closed boreal forest to the treeless tundra (i.e. where trees, irrespective of size, cease to occur). In most regions of the circumarctic area, the FTE, according to this definition, entirely overlaps the subarctic shrub zone which is thus considered to be part of the FTE vegetation. The FTE thus spans the forest line (defined by stand density), the tree island line (defined by tree clones or small tree patches), the treeline (defined by height of erect trees), the krummholz line (defined by dwarfed shrubby tree growth forms) and the tree seedling line (defined by the most advanced location of tree species). Details for each site are given in Data S1.

FIGURE 1 Location of sites and regionalization of qualitative behaviour data for the circumarctic forest-tundra ecotone (FTE). Circles indicate sites and light green shading the area from which data were sought. Dashed lines and italic typeface show the nine geographical areas into which the data were originally divided, while bold lines and large typeface show the four regions adopted following principal component analysis of 20th century climate trends (CRU TS3.21: Harris et al., 2014). Site colours show qualitative FTE behaviour. Summary for each behaviour type per region is given in the inset table, where AWCC denotes Alaska, Western & Central Canada, EC Eastern Canada, WEA Western Eurasia and SIB Siberia. Individual site information is given in Data S1. For ease of visualization green circles were made 10% smaller than yellow and red circles, and some points have been slightly offset from their true positions (provided in Data S1)



The assembled data represent recent studies (i.e. conducted after 1980) of 20th century changes in the FTE that include information on qualitative behaviour and/or rates of FTE movement. The rate of advance (m/year) was either retrieved directly from the publications or calculated from displacement and time information provided in the publications (Data S1). Rate estimates are available for a subset of the sites ($n = 79$) and include both altitudinal ($n = 60$) and latitudinal ($n = 19$) rates. Furthermore, site information on behaviour and rates of change had to be based on ecologically sound background data including monitoring, repeat photography, detailed age structure analyses, or high-resolution remote sensing (aerial photography or high-resolution satellite imagery such as QuickBird). General statements were not sufficient for inclusion, and publications dealing with radial growth, recovery from disturbance, response to glacial retreat, or longitudinal FTE movements were not included. Entries that fulfilled the required criteria included single locations, larger landscape sections, and multiple locations (in some cases, more than 100) within the same area. Although some sites were based on several within-site locations, each listed site was given equal weight in the analyses. Publications dealing with more than one tree species per site were included as one site per species when information was given separately.

To be included in our study, data had to be acquired from sites located beyond the closed boreal forest and north of region-specific latitudes (Data S1; Figure 1) chosen to restrict and enclose the full latitudinal range of the subarctic FTE. We relaxed this latitudinal restriction to include high-quality data from nine sites just south of the defined limits: three in Fennoscandia and six in the Urals (Data S1; Figure 1). The assembled sites represent nine geographical areas separated based on longitude (Data S1; Figure 1).

2.2 | Climate trends and regionalization of the assembled sites

Climate history data for the 20th century were extracted from the 0.5-degree gridded time-series dataset CRU TS3.21 (Harris, Jones, Osborn, & Lister, 2014) generated by the University of East Anglia Climate Research Unit and downloaded from the British Atmospheric Data Centre (<http://badc.nerc.ac.uk>) as monthly elements (temperature and precipitation values) for the years 1901–2000. These were used to generate gridded rates of change for the periods 1901–2000 and 1951–2000, using linear least-squares regression, for every month. These two time periods were chosen to capture non-uniformity in climate change during the 20th century as a whole and during the latter half (e.g. ACIA, 2005). Data were then extracted from the grid cell nearest to each site. Each site was thus represented by 48 monthly climate trend variables (2 elements \times 2 time periods \times 12 months), which were designated by month and also by the terms T100, T50, P100, and P50, where *T* and *P* refer to temperature and precipitation, respectively, and 100 and 50 refer to the periods 1901–2000 and 1951–2000, respectively. Monthly climate trend variables were in addition used to calculate seasonal and annual trends per element and time period. The site data were then

grouped based on similar climate trends using principal component analysis (PCA) following standardization (*z*-score) of variables. This regionalization of the data is thus independent of the original division into nine geographical areas.

2.3 | Statistical analysis

Qualitative statements on the 20th century FTE behaviour for the 151 sites included eight different behaviour denominations (Data S1) that we grouped into three types of behaviour for the analyses: advancing (including advancing and advancing-infilling denominations), stationary (infilling, infilling-stationary, and stationary), and retreating (infilling-retreating, stationary-retreating, and retreating). Behaviour types were then tested for regional differences in their relative proportions (chi-squared test), and—without regard to region—for differences in climate trends (Mann–Whitney–Wilcoxon test). The two types of sites with quantitative statements on the 20th century behaviour of the FTE (60 altitudinal sites and 19 latitudinal sites; Data S1) were analysed separately for quantitative behaviour. However, we also considered production of a combined dataset in which altitudinal rates were converted to equivalent latitudinal rates. For this, we considered two possible conversion factors: (a) theoretical, based on lapse rates and (b) empirical, based on our own data (Data S1). The theoretical approach compares the distance towards north, on flat ground, where the same decrease in mean annual temperature is found as when going some distance upslope. It is therefore given by the ratio of the altitudinal lapse rate (typically 6.5°C/km; Houghton, 2002) and the latitudinal temperature gradient (typically 0.0069°C/km; Jump, Mátyás, & Peñuelas, 2009). The ratio between these is of the order of 1,000. The assembled empirical altitudinal and latitudinal data, however, indicate a ratio of around 100 (cf. Section 3.3 and Data S3). The discrepancy between the two estimates and the associated interpretation of the ability of the FTE to advance when driven by climate change are discussed below. These quantitative data were tested for regional differences (Mann–Whitney–Wilcoxon test), and—without regard to region—for correlation with 20th century climate trends (Spearman rank correlation) separately for the two time periods. Statistical analysis of the data was performed in GNU Octave v. 4.0.3 (Eaton, Bateman, Hauberg, & Wehbring, 2015).

3 | RESULTS

3.1 | Regionalization of sites by 20th century climate history

The 151 sites were classified into four main regions based on PCA of the site-based climate trend variables (Figure 2a–c). The first four principal components accounted for 28.5, 14.8, 12.1, and 9.3% (sum = 64.7%; Data S2) of the total variance, respectively, with PC1 broadly corresponding to the P100 climate trend variable (Figure 3a) during non-growing season months (Data S2). Sites from

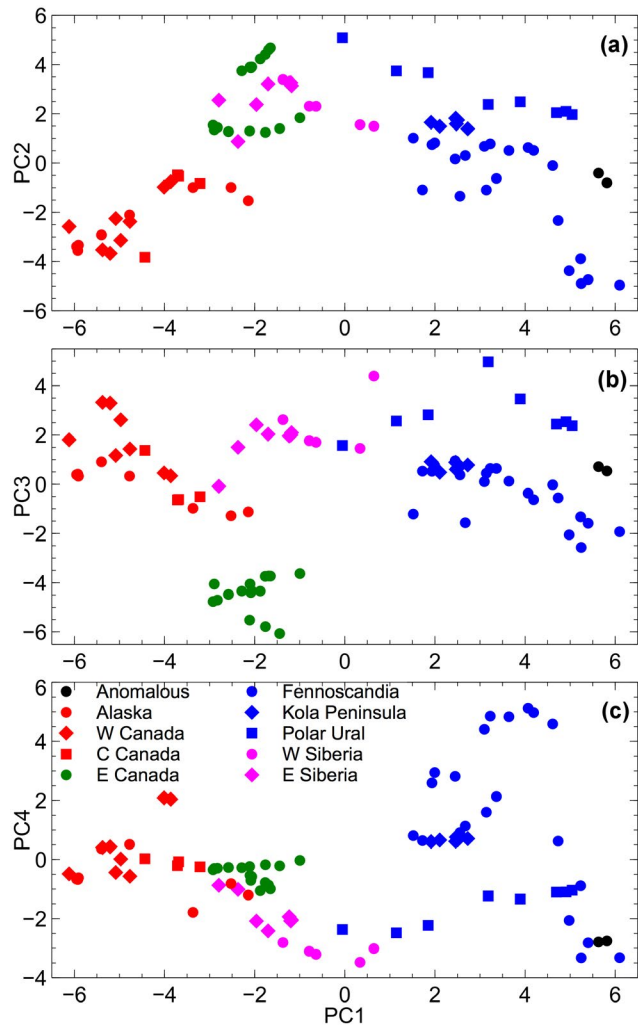


FIGURE 2 Scattergrams of the first four principal components for all 151 sites, calculated based on their monthly climate histories (CRU TS3.21; Harris et al., 2014) over the periods 1901–2000 and 1951–2000. The sites were initially grouped according to the nine geographical areas defined by colours and symbols. The different colours of symbols show the final grouping of the sites into four regions: Alaska, Western & Central Canada (AWCC: red), Eastern Canada (EC: green), Western Eurasia (WEA: blue), Siberia (SIB: magenta). Two ‘anomalous’ sites (black) originally part of the Western Siberia area were omitted from region-specific analyses

the longitude-based geographical areas defined as Alaska, Western Canada and Central Canada (henceforward AWCC), Eastern Canada (EC), and Western and Eastern Siberia (SIB) formed three separate groups, all characterized by negative PC1 scores (Figure 2a–c). The EC and SIB regions were also differentiated by PC3 (Figure 2b), which broadly corresponds to temperature trends (T100 and T50; Figure 3a,b) in the spring (Data S2). Sites from geographical areas defined as Fennoscandia, the Kola Peninsula, and the Polar Ural areas formed a fourth region, Western Eurasia (WEA), characterized by positive PC1 scores (Figure 2a–c). Two sites originally belonging to Western Siberia (Dudinka and Noril’sk, Data S1) were inconsistent with this grouping due to anomalous climate trends (Figures 2a–c

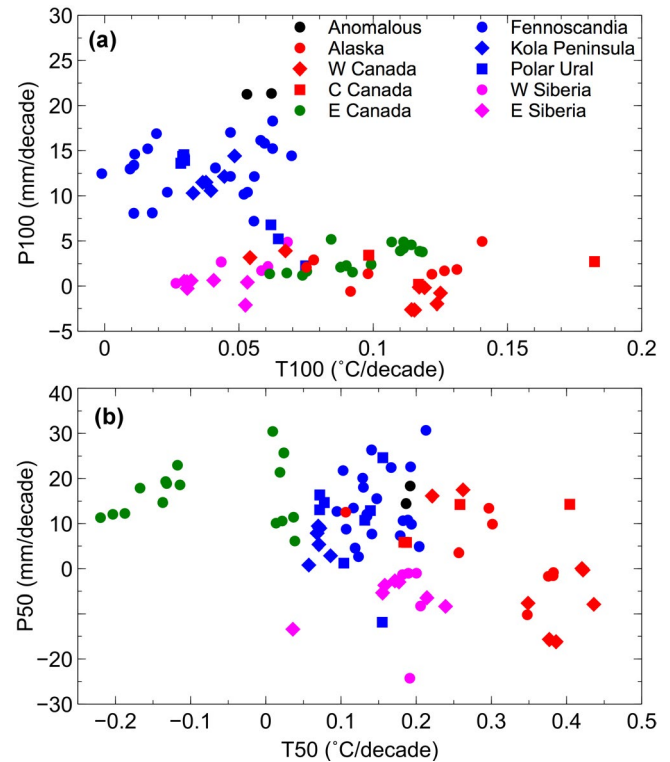


FIGURE 3 Site-level trends in annual mean temperature (x-axes) and annual total precipitation (y-axes; CRU TS3.21; Harris et al., 2014) over the periods 1901–2000 (a) and 1951–2000 (b). The key shows original geographical subdivision of sites (cf. Figure 1 and Data S1) with the regionalization of sites represented by the four colours. Two anomalous sites originally part of Western Siberia are shown in black. *T* and *P* denote temperature and precipitation, ‘100’ and ‘50’ denote the periods 1901–2000 and 1951–2000, respectively

and 3a,b). These two sites were excluded from all subsequent region-specific analyses.

Site-level trends in annual mean temperature and precipitation tested over the 100- and 50-year periods (Figure 3a,b) further reveal that the WEA region, which has high values of PC1 (Figure 2a–c), differs from the others in respect of long-term precipitation increase (P100) but not in the shorter term (P50; Figure 3b). This change in precipitation over the 1901–2000 period is characteristic of most months, with emphasis on October and December, but also includes an apparent precipitation decrease for September (Figure 4c–d). The EC and AWCC regions are distinguished by, respectively, low and high values of T50 (Figure 3b), the low values being associated with the January–March period and the high values with combined winter (DJF) and early-mid-summer (JJ) temperature increase (Figure 4a–b).

3.2 | Qualitative behaviour of FTE (movement status of the boundary)

The assembled site data show that a small majority (52.3%) display advancing behaviour (Figure 1), while 45.7% shows stationary behaviour, and only a few sites (2.0%) show retreating behaviour. All

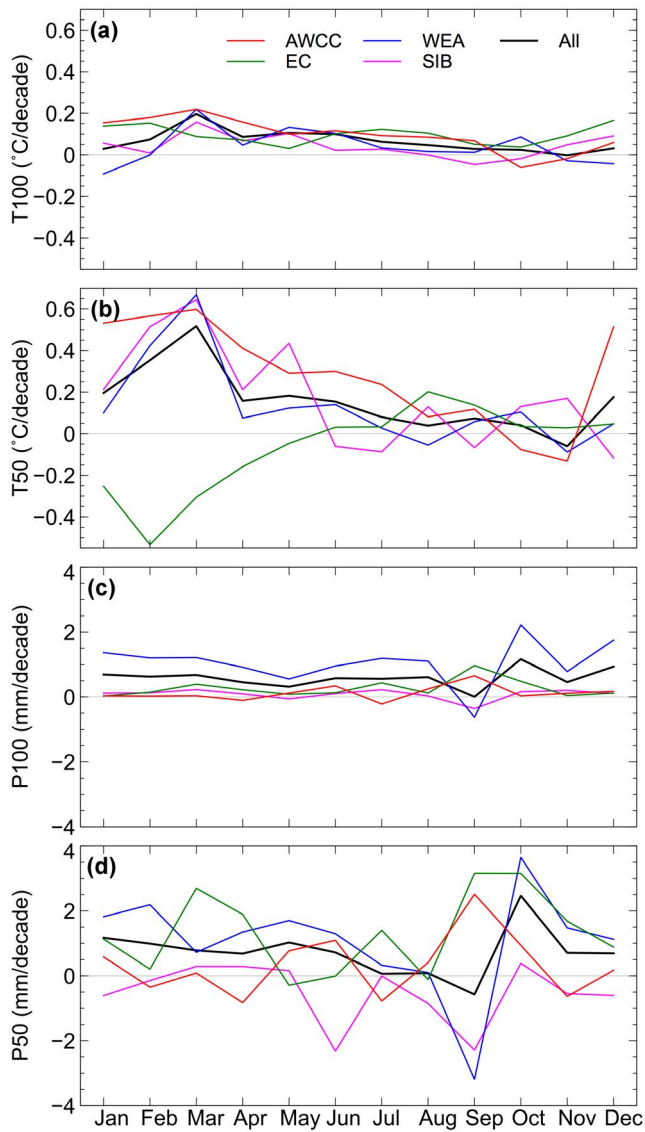


FIGURE 4 Climate trend values (CRU TS3.21; Harris et al., 2014) per month for analysed sites aggregated by region (coloured lines) and mean for all sites (black line). *T* and *P* denote temperature and precipitation, '100' and '50' denote the periods 1901–2000 and 1951–2000 respectively

regions except SIB show broadly similar distributions of behaviour (Figure 1). However, the number of sites in SIB was small, and a chi-squared test showed that it did not differ significantly from the mean over all sites ($\chi^2 = 2.09, 2 \text{ df}, p = .35$).

Twentieth century climate trend variables compared for advancing and stationary behaviours, without regard to region, show broadly similar temperature and precipitation variations through the year, though significant differences are evident during some months of the year (Figure 5a–d). Generally, these differences occur in spring and early summer for temperature (T100) and in spring and summer (P50) and early autumn for precipitation (P100 and P50). The months with the strongest recorded climate trends over both time periods, March for temperature and October for precipitation, show the same impact for the two FTE behaviour categories.

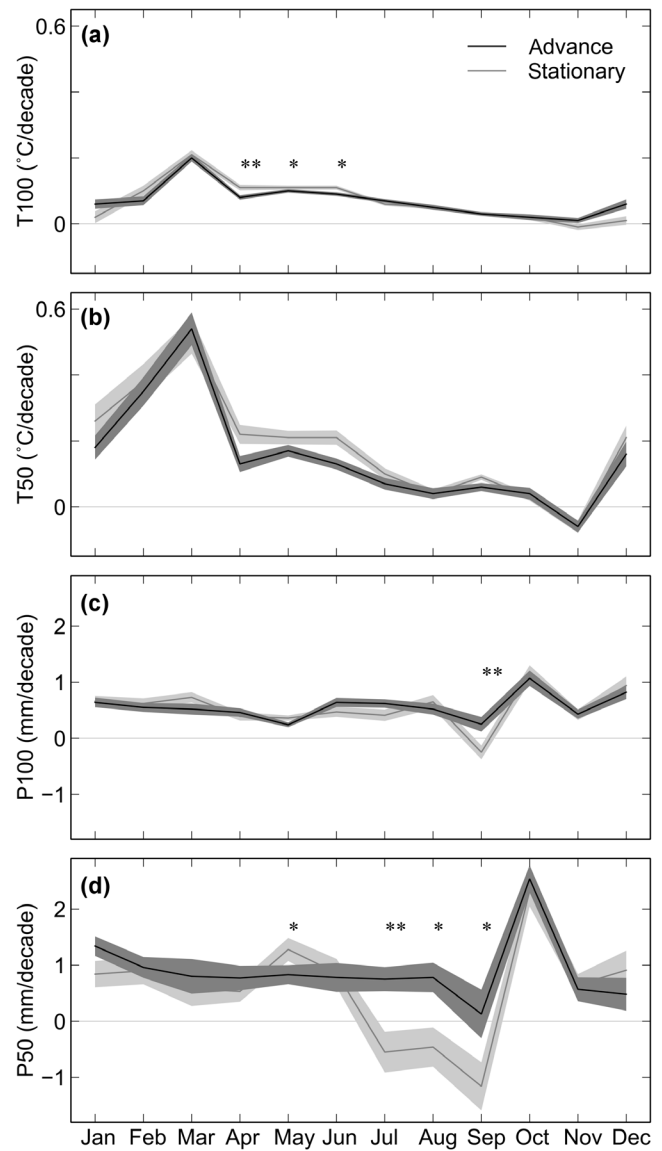


FIGURE 5 Mean climate trends per decade for each month of the year separated by sites with advancing (dark grey) and stationary (light grey) forest-tundra ecotone (FTE) behaviour (trends for sites with retreating FTE are not shown due to their limited number). Shaded areas show the estimated uncertainties ($\sigma/\sqrt{(n - 1)}$) in the mean values. Significant differences (two-tailed Mann-Whitney-Wilcoxon test) between advancing and stationary behaviour are shown as follows: $p < .05$ (*) and $p < .01$ (**). *T* and *P* denote temperature and precipitation, '100' and '50' denote the periods 1901–2000 and 1951–2000, respectively. Climate trend data are derived from CRU TS3.21 (Harris et al., 2014)

3.3 | Quantitative behaviour of FTE (rate of change of position)

The advance rate averaged over all sites for which quantitative data were available ($n = 79$) was 0.48 m/year for altitudinal sites ($n = 60$) and 37 m/year for latitudinal sites ($n = 19$). Using only sites included in the advancing behaviour type ($n = 46$), the averages were

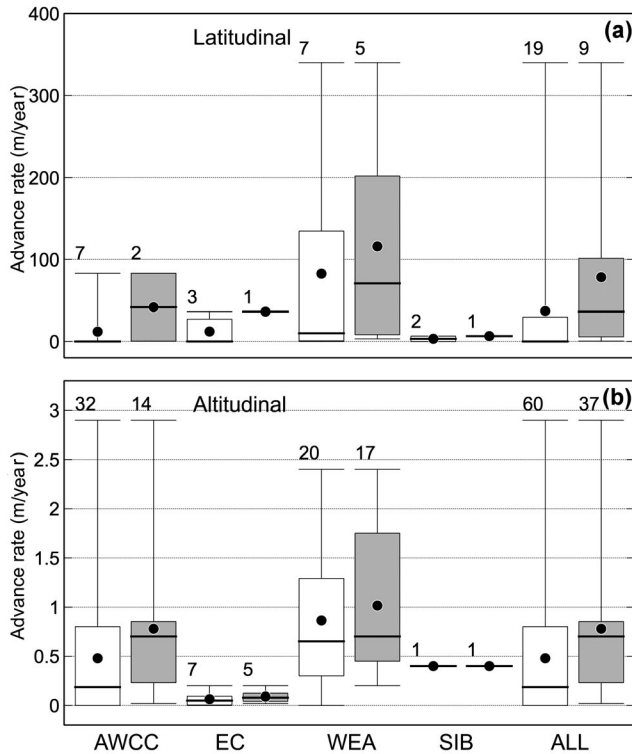


FIGURE 6 Box-and-whisker plots summarizing quantitative latitudinal (a) and altitudinal (b) advance rates by region and in total (for region names see Figure 1). Boxes show interquartile ranges, whiskers maximum and minimum values, bold lines medians, and dots means. White boxes include all site-level data points for a region; grey boxes include only sites exhibiting positive advance rates. Numbers of sites are shown adjacent to each plot

0.78 m/year ($n = 37$) and 79 m/year ($n = 9$), respectively. The ratio of these values would define an empirical factor used to convert altitudinal to equivalent latitudinal advance rates in a combined data comparison (see Data S3 for details). There was no evidence that the ratio varied among regions (Data S3), although the numbers of sites with quantitative rate data were small for the EC and SIB regions. Regionalization of the data suggests that the advance rates in AWCC and WEA are higher than those in EC and SIB (Figure 6a,b). Advance rates in EC are significantly less than in AWCC and WEA, but not compared to SIB. Maximum observed advance rates show the same regionalization, being around 250–350 m/year in AWCC and WEA, and around 40 m/year in EC.

In total, significant associations were found between circumpolar FTE advance rates and climate trend variables in almost all months of the year (Data S4), but the strength of the association of individual months and FTE advance varied among climate elements and time periods (Figure 7a,b). In general, correlations between FTE advance and temperature trends over the 20th century (both periods) were either non-significant or negatively correlated for all months except October (T100). This indication of October's importance was also evident through significant positive correlation between latitudinal advance and precipitation trend (both periods). Unequivocally strong

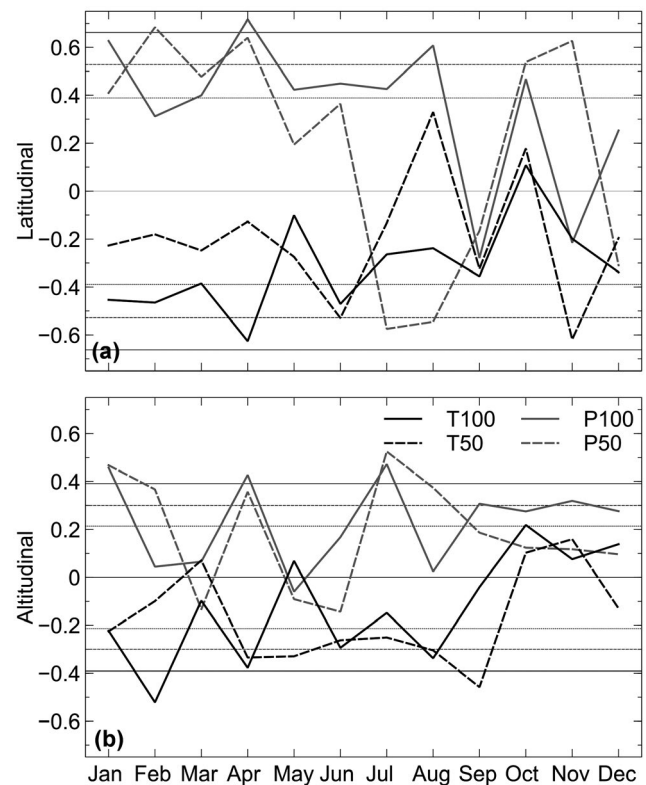


FIGURE 7 Spearman rank correlation coefficients between advance rates and monthly climate trend variables for latitudinal (a) and altitudinal (b) sites separately. The horizontal dotted, dashed and solid lines show the confidence limits for significant correlation at $p = .05$, $.01$, and $.001$, respectively. *T* and *P* denote temperature and precipitation, '100' and '50' denote the periods 1901–2000 and 1951–2000, respectively. Climate trend data refer to CRU TS3.21 (Harris et al., 2014)

correlations, that is, those whose signs were consistent between latitudinal and altitudinal datasets and whose statistical significance remained high in all cases, were predominantly related to precipitation trends rather than temperature trends (Figure 7a,b). In general, precipitation trends over the period 1951–2000 were significantly positively correlated with FTE advance rate for a wide range of months, primarily January, February, and April. Over the period 1901–2000, the main months with positive correlations between precipitation trend and FTE advance rate were January, April, July, and October.

4 | DISCUSSION

Although progressive advance of the high-latitude FTE is a common assumption in global change assessments (ACIA, 2005; Alley et al., 2007; Larsen et al., 2014), the observed advancing behaviour for only around half of our sites is consistent with findings integrated worldwide from high- and low-latitude sites (Harsch et al., 2009; Mamet et al., 2019). This phenomenon of non-advancing behaviour at some sites applies not only to the circumpolar FTE as a whole but also to different regions of the circumpolar area individually,

despite different climate histories over the 20th century. Although this possibly suggests non-climatic influences on the behaviour of the FTE, significant correlations with climate history are present both for qualitative and quantitative behaviours. However, quantitative behaviour based on the presented empirical estimates discloses large discrepancies with CCV-based estimates and the predictions of ENMs.

4.1 | FTE behaviour and climate history association

The most obvious differences in climate history among sites showing different qualitative behaviours relate to temperature in spring and early growing season, and to precipitation in mid- to late growing season and early autumn. The quantitative behaviour, on the other hand, relates most strongly to the history of late growing season and mid-autumn temperature and to early spring and early- to mid-growing season precipitation. However, for both behaviours, the role of precipitation variables, rather than temperature, is emphasized and elucidates the otherwise seemingly opposite climate history association, regarding climate element, for the two behaviour types. Although hard to disentangle, both behaviour types are dependent on establishment and growth of tree seedlings, at the same time as these processes might be driven by different climate conditions (including weather events; Gamache & Payette, 2005; Holtmeier & Broll, 2005). For example, drought conditions during the growing season might be detrimental to establishment but have no or little impact on growth of deeper-rooted saplings. Hypothetically, the shown advancing behaviour, hindered by temperature increase in spring-early growing season and precipitation decrease in late growing season to early autumn, could relate to unfavourable, possibly dry, conditions for seedling establishment. Furthermore, the positive associations throughout most of the year for precipitation and rate of advance might be linked to survival- and growth-promoting moisture during the growing season and presence of snow cover during winter months (Holtmeier & Broll, 2005). Growth promotion by winter snow is generally mediated by soil insulation and thereby warmer soil conditions persisting into the start of the growing season, melt-water enrichment of soil moisture in the early growing season, and protection from wind abrasion during winter (Fr chet te, Ensminger, Bergeron, Gessler, & Berninger, 2011; Hagedorn et al., 2014; Sturm et al., 2001; Vaganov, Hughes, Kirilyanov, Schweingruber, & Silkin, 1999).

Although the associations between FTE behaviour and climate history are generally similar for the two investigated time periods, the analyses reveal some temporal differences, with full-century temperature and half-century precipitation changes characterizing the qualitative behaviour. This difference in association is consistent with high-latitude climate change characteristics since the early 20th century (i.e. temperature increase composed of one early-century warming period and one late-century warming period separated by a cooling period, and precipitation showing a gradual increase with emphasis on the latter half of the century; ACIA, 2005). The

quantitative behaviour, on the other hand, shows no obvious systematic differences between tested periods when all sites were analysed together (cf. Figure 7a,b). However, some region-specific differences can be inferred from the regional grouping based on site-level climate trend data (shown in Figure 3a,b). The most evident examples are the EC and WEA regions with, respectively, the lowest and highest advance rates (cf. Figure 6a,b). Climatically, the EC region is distinguished from other regions by the least positive, or even negative, annual mean temperature change over the half-century period, and the WEA region by high rates of precipitation increase over the full-century period. Although sample numbers were too small to inform robust statistical conclusions, these regional differences are ecologically plausible, since low or negative temperature change would have limited effect on advance rate, but precipitation increase in a warming climate would have a positive influence.

4.2 | Quantitative FTE behaviour and CCV values

The empirically based mean ratio between latitudinal and altitudinal FTE advance rates of 100 deviates markedly from the ratio between the atmospheric temperature lapse rate and the latitudinal temperature gradient, which is of the order of 10^3 (see Section 2.3). This large discrepancy, see also Data S3, points to the fact that mean temperature alone is not an adequate controlling factor in determining the location of the FTE. Since the temperature-based CCV is given by the ratio of the rate of temperature increase (typically 10^{-2} °C/year over the 20th century; Figure 3a) to the latitudinal gradient, 20th century CCVs were of the order of 10^3 m/year (see also Timoney et al., 2018). Observed latitudinal advance rates (Figure 6a) are thus almost two orders of magnitude smaller than typical CCVs for the studied sites during the 20th century. Observed altitudinal advance rates (Figure 6b), on the other hand, of the order of 1 m/year, indicate a magnitude agreement with typical CCV values (further discussed below).

The large mismatch between empirical northward movement rates and CCVs points to the importance of considering migration lags in models of vegetation response to climate change. Adoption of concepts based on equilibrium between the contemporaneous distribution of vegetation boundaries and climate variables would be misleading as they inevitably assume there are no limitations on movements other than some major climate variables (Ga uz re, Iversen, Barnagaud, Svenning, & Blonder, 2018). However, the ability to predict migration lags, of the FTE, or transition zones in general, commonly suffers from lack of knowledge or reliable data about factors naturally controlling vegetation dynamics and range expansion (Hofgaard et al., 2013; Holtmeier & Broll, 2005; van Bogaert et al., 2011), including climate change-driven alteration of important abiotic and biotic disturbance agents (Pureswaran et al., 2015; Seidl et al., 2017). The assembled site data comprise authors' conclusions or assumptions about causes of observed behaviour, such as changed growing season length, non-growing season effects, and temperature and precipitation changes but also non-climatic variables such

as herbivory, fire, aspect, and recruitment. Lack of recruitment as a cause of non-advancing behaviour was found around the entire circumarctic area. However, the non-advancing behaviour was also observed in areas with frequent recruitment. This seemingly contradictory finding pertains in particular to areas where the dominant FTE tree species is an important food source for herbivores, preventing long-term survival and growth (Aune, Hofgaard, & Söderström, 2011; Cairns & Moen, 2004; Olofsson et al., 2009; Vindstad, Jepsen, Ek, Pepi, & Ims, 2018) and points to the difficulty in differentiating dispersal-maintained sink populations from expanding populations (Mathisen, Mikheeva, Tutubalina, Aune, & Hofgaard, 2014).

The notion that mean FTE advance rates could even approximately keep pace with changing climate seems ecologically unrealistic when considering dispersal limitations (Jump et al., 2009; Kambo & Danby, 2018). While most tree species characterizing the circumarctic FTE have winter-dispersed seeds, which may promote long-distance dispersal, the velocity of FTE propagation is not strongly related to range of seed dispersal (Aune et al., 2011; Hofgaard et al., 2013; Holtmeier & Broll, 2005). The main limitation to the ability of trees to track climate change is linked to viable seed arrival at sites promoting establishment, survival, and growth over the decade-to-century timescale. These sites will be geographically limited to specific locations with favourable topographic, edaphic, or microclimatic conditions (Holtmeier & Broll, 2005; Kullman, 2010). This, and the time required to reach tree size and the seed-producing stage while withstanding Arctic winter supranival conditions, varies spatially and temporally due to a multitude of abiotic and biotic factors (Holtmeier & Broll, 2005). As a result, the FTE is characterized by high seedling/sapling turnover, with mostly ephemeral seedling cohorts (Aune et al., 2011; Holtmeier & Broll, 2005). Still, many FTE tree species are, when established, well adapted to track changes through their longevity and/or vegetative regeneration capacity, which favour survival during less favourable periods and responsiveness to improved conditions (Payette et al., 2001). However, the spatio-temporal heterogeneous combination of a large number of climatic and non-climatic variables, including episodic disturbances (e.g. insects and fire) and changed disturbance regimes, impedes a rapid northward movement of the circumarctic FTE (Holtmeier & Broll, 2005; Kullman, 1986; Payette et al., 2001; Sirois & Payette, 1991; Timoney et al., 2018). Consequently, empirically based FTE advance rates lag behind both typical CCV values and estimated displacement capacities for trees (Iverson, Schwartz, & Prasad, 2004; McLachlan, Clark, & Manos, 2005; Meier, Lischke, Schmatz, & Zimmermann, 2012; Nathan et al., 2011).

4.3 | Implications of behaviour–climate association in the light of future climate change

The question of the maximum displacement rate for circumarctic forest appears to be rather open. IPCC AR5 assumes (Settele et al., 2014) that trees can migrate at up to around 1,500 m/year (i.e. approximate upper limit of the estimated 95% confidence

interval) with a median of around 100 m/year, but does not distinguish among species or biomes. Previous estimates of expansion rates after the last ice age of around 1 km/year (Clark, 1998) are sensitive to assumptions about refugia and have been revised downwards to around 250 m/year (Cheddadi et al., 2014; Feurdean et al., 2013) or as low as 100 m/year (Meier et al., 2012; Nathan, 2006; Thompson & Katul, 2008). Consequently, our results for latitudinal FTE movement would not contradict predictions of models that imposed maximum advance rates of the order of 100 m/year.

Advance rates of altitudinal FTEs could, however, possibly be more in balance with CCVs. A reason for this might be the distance propagating seeds have to travel and growth rate of established seedlings. A typical 20th century CCV of the order of 10^3 m/year (cf. above) on flat terrain would correspond to an upslope advance rate of the order of 1 m/year (which is similar to empirical-based values), using the theoretical altitude-for-latitude ratio of around 1,000 (Jump et al., 2009). Furthermore, if a typical tree takes around 40–50 years to grow from germination of seed to tree-size (Aune et al., 2011; Dalen & Hofgaard, 2005; Hofgaard, 1993a), a climate–FTE equilibrium would require annual seed dispersal and successful seedling establishment over distances of typically 50 altitudinal metres for altitudinal advance, but 50 km for latitudinal advance. Although these numerical values are simply order-of-magnitude estimates, and do not take tree species-related spatiotemporal variation in seed production into account (Hofgaard, 1993b; Holtmeier & Broll, 2005; Houle & Fillion, 1993; Sirois, 2000), they demonstrate that if viable seed dispersal is the rate-limiting process (Brown et al., 2019; Wieczorek et al., 2017), it is reasonable to suppose that while climate-driven altitudinal FTEs may be able to keep pace with climate change at a centennial scale and at optimal sites (Kullman, 2018), latitudinal FTEs are unable to do so.

Consequently, it would be realistic to conclude that ENMs predicting disappearance of up to around 50% of the current arctic tundra over the 21st century through encroachment by FTE vegetation (Callaghan et al., 2005; Pearson et al., 2013) are, as previously shown for restricted geographical areas (Hofgaard et al., 2013; van Bogaert et al., 2011), likely to be severe overestimates at the circumpolar level. Process-based models capable of more realistically representing the response of high-latitude vegetation to changing climatic conditions need to consider climatic as well as non-climatic limitations on movement of biome transitions. In addition, 21st century FTE ecosystem responses might possibly be controlled by novel biotic and abiotic disturbance regimes (Macias-Fauria et al., 2012; Payette et al., 2001). Incorporation of both biotic and abiotic aspects would increase the utility of models of global vegetation distribution regarding, inter alia, disappearance of arctic tundra and associated land-atmosphere feedbacks. Advancing tall arboreal or woody vegetation provides contrasting climate feedbacks through carbon sequestration (cooling) and reduced surface reflectance (warming; Chapin III et al., 2005; Pearson et al., 2013). The net climate feedback associated with FTE advance would, according to recent model predictions,

intensify warming, largely mediated through change to taller, aerodynamically rougher and darker vegetation (Bonfils et al., 2012; de Wit et al., 2014; Loranty, Berner, Goetz, Jin, & Randerson, 2014).

The observed lack of uniformly advancing behaviour of subarctic forests, and advance rates so far below the velocity of climate change, makes it unreasonable to believe that northward movement of the subarctic FTE as a whole or regionally could keep pace with climate change within the 21st century. Non-climatic factors (such as fire and herbivory) controlling the dynamics of vegetation distribution need more attention to guide the development of quantitative process-based models capable of describing the response of vegetation distribution to changing climate—for the subarctic FTE and global vegetation transitions in general. This will require more extensive empirical datasets capturing both mechanistic and correlative understanding of intrinsic processes.

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AUTHORS' CONTRIBUTIONS

Project conceived and designed by A.H. and W.G.R. Unpublished data provided by A.H. and I.M. Data analyses carried out by W.G.R. and A.H. with support from O.T. and Z.S. Manuscript preparation led by A.H. and W.G.R., with support from all co-authors. Final version of the manuscript read and approved by all co-authors.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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