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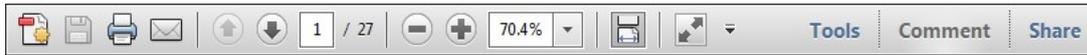
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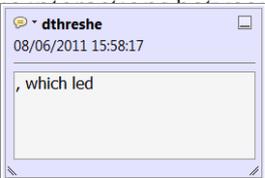### 1. Replace (Ins) Tool – for replacing text.

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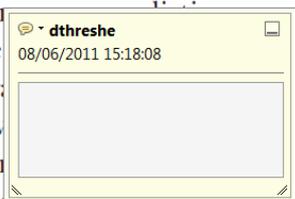### 4. Add sticky note Tool – for making notes at specific points in the text.

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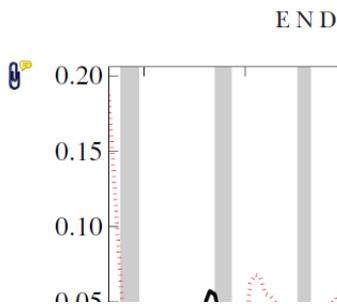
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PRIMARY RESEARCH ARTICLE

WILEY **Global Change Biology**

Higher climate warming sensitivity of Sibirian larch in small than large forest islands in the fragmented Mongolian forest steppe

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Abstract

Forest fragmentation has been found to affect biodiversity and ecosystem functioning in multiple ways. We asked whether forest size and isolation in fragmented woodlands influences the climate warming sensitivity of tree growth in the southern boreal forest of the Mongolian *Larix sibirica* forest steppe, a naturally fragmented woodland embedded in grassland, which is highly affect by warming, drought, and increasing anthropogenic forest destruction in recent time. We examined the influence of stand size and stand isolation on the growth performance of larch in forests of four different size classes located in a woodland-dominated forest-steppe area and small forest patches in a grassland-dominated area. We found increasing climate sensitivity and decreasing first-order autocorrelation of annual stemwood increment with decreasing stand size. Stemwood increment increased with previous year's June and August precipitation in the three smallest forest size classes, but not in the largest forests. In the grassland-dominated area, the tree growth dependence on summer rainfall was highest. Missing ring frequency has strongly increased since the 1970s in small, but not in large forests. In the grassland-dominated area, the increase was much greater than in the forest-dominated landscape. Forest regeneration decreased with decreasing stand size and was scarce or absent in the smallest forests. Our results suggest that the larch trees in small and isolated forest patches are far more susceptible to climate warming than large in continuous forests pointing to a grim future for the forests in this strongly warming region of the boreal forest that is also under high land use pressure.

KEYWORDS
boreal forest, deforestation, forest regeneration, global warming, habitat fragmentation, missing rings, Siberian larch (*Larix sibirica*), tree ring analysis

1 | INTRODUCTION

Effects of global climate warming on boreal forests have been reported from different areas of this vegetation belt (Lloyd & Bunn, 2007). Rising temperatures can either lead to increased productivity and the advancement of treelines if low summer temperatures are limiting, or result in decreased productivity and even increased rates of tree mortality, if the vegetation is limited by moisture availability.

Buermann et al. (2014) showed that moisture limitation has become increasingly relevant in the recent past. Climate-response analyses of tree ring width (Barber, Juday, & Finney, 2000) as well as analyses of drought-induced missing ring frequency (Khishigjargal, Dulamsuren, Leuschner, Leuschner, & Hauck, 2014), tree mortality (Peng et al., 2011), forest regeneration (Bond-Lamberty et al., 2014), and treeline position (Kullman & Öberg, 2009) have been published repeatedly that elucidate the response of boreal forest trees to different climatic trends.

Interaction of other factors with the climate warming sensitivity of boreal forests is less well studied. Probably most attention has been paid to the interaction of climate warming with fire and their combined effect on vegetation. While increased drought intensity increases fire frequency and intensity (Girardin et al., 2009), the replacement of conifers by broadleaved pioneer stands following the disturbance reduces the likelihood and the effect of forest fires (Terrier, Girardin, Périé, Legendre, & Bergeron, 2013). The impact of insect herbivores on boreal forests is usually thought to increase negative effects of climate warming, as herbivore life cycles are accelerated and overwinter survival is increased (Ayres & Lombardero, 2000). The ability to defend herbivores of conifers is affected by drought, as a reduced turgor of xylem parenchyma cells decreases, although not the production of resin, but the pressure gradient along which it is transported to wounded tissue (Rosner & Hannrup, 2004). Climate warming can also establish new herbivore–host plant relationships through asynchronous range shifts (Hódar & Zamora, 2004).

The structure of forest stands also interacts with climate warming, as stand structure influences the competition between trees for water. Therefore, stand density is generally inversely correlated with water availability (McDowell & Allen, 2015). This was also shown in the boreal forest of Mongolia, where trees at forest edges with reduced stand density had less tense water relations and higher tree ring widths than in the forest interior (Dulamsuren, Hauck & Leuschner, 2010; Dulamsuren, Hauck, Khishigjargal, et al. 2010; Chenlemuge et al., 2015). The influence of other stand-structural characteristics on the climate warming sensitivity of forests is much less explored.

We addressed the question how forest fragmentation interacts with the sensitivity of moisture-limited boreal forest stands to global climate warming. The forest-steppe ecotone of Mongolia is characterized, like other forest-steppe ecotones in mountainous terrain, by a mosaic of boreal forest patches at the moistest places on north-facing mountain slopes and grasslands on south-facing slopes. This natural pattern creates forest islands of varying size, while the forest stands have been additionally fragmented by human activities due to industrial logging, forest fires, and the combined impact of wood extraction and forest grazing by mobile pastoralists (Erdenechuluun, 2006; Lkhagvadorj, Hauck, Dulamsuren, & Tsogtbaatar, 2013a). Hansen, Potapov, and Moore (2013) identified Mongolia as one of the world's countries with the highest rates of recent net loss of forest area.

Forest fragmentation results in the reduction of stand size and also in the isolation of forest stands. The effects of forest fragmentation or habitat isolation in general have mostly been studied with respect to changes in biodiversity (Robinson et al., 1992; Fahrig, 2003). In addition to isolation effects, forest fragmentation enhances edge effects with increasing temperature extremes and a drier microclimate found in forest islands as compared to the interior of continuous forest stands (Debinski and Holt, 2001; Saunders, Hobbs, & Margules, 1991). Fragmentation may also affect the nutrient status of soil and plants mediated via differences in microclimate, atmospheric inputs, and differences in decomposition rate (Bierregaard, Lovejoy, Kapos, dos Santos, & Hutchings, 1992; Didham, 1997).

There are several potential factors in small forest patches of the Mongolian forest steppe that could differ from the conditions in continuous forests and might influence the trees' vigor and productivity. These factors include microclimate, as temperature should reach more extreme maxima and minima in small forests, whereas air humidity and soil moisture should be higher and less variable in the interior of continuous forests (Chen, Franklin, & Spies, 1995; Chen et al., 1999). Due to the characteristic type of land use in the Mongolian forest steppe with mobile pastoralists, who house with their livestock in the grasslands around the forests and make their living off the use of local ecosystem services, forest stand size can also be assumed to influence land use intensity. Small forests are likely to be more severely affected by forest grazing which contributes to the suppression of forest regeneration (Khishigjargal, Dulamsuren, Lkhagvadorj, Leuschner, & Hauck, 2013). Furthermore, pastoralists in Mongolia satisfy their needs for fuel and construction wood preferentially from forests in the neighborhood of their dwellings and from forest edges in particular (Dulamsuren, Khishigjargal, Leuschner, & Hauck, 2014). This practice should result in higher anthropogenic disturbance of the stand structure with decreasing stand size.

To study the putatively complex interaction of forest fragmentation with productivity and stand structure, we conducted tree ring analyses and stand surveys in forests of Siberian larch (*Larix sibirica*) of varying stand size in the Mongolian forest steppe (Fig. S1 in the Supporting Information). The objective of our study was to test the hypotheses that (1) decreasing stand size increases climate sensitivity and thus the susceptibility to summer drought of radial stem increment (2) the frequency of drought-induced missing rings increases with decreasing stand size, and (3) forest regeneration success increases with increasing stand size. In addition to stands of varying size, we compared forest islands of the same size in a forest-dominated subregion with isolated stands in a grassland-dominated subregion to test the hypothesis (4) that forests in the grassland-dominated landscape are more sensitive to variation in climate, as climatic parameters can be expected to be more variable here than in forest-dominated areas of the forest-steppe ecotone. Validation of our hypotheses would imply that forest fragmentation would aggravate the already widespread drought-induced reductions in forest productivity in moisture-limited boreal forests.

2 | MATERIALS AND METHODS

2.1 | Study area

Field work was carried out in August 2014 near Tosontsengel (Zavkhan province, 48°45′N, 98°16′E, 1700 m a.s.l.) in the forest steppe of Mongolia, c. 630 km W of Ulan Bator and 550 km SW of Lake Baikal. The Inner Asian forest-steppe regions form the southernmost part of the spacious Eurosiberian boreal forest region. Except for some temperature-limited forests that are mostly located near the alpine treeline (Jacoby, D'Arrigo, & Davaajamts, 1996; Chen et al., 2012; Dulamsuren et al., 2014), most studied forests in the forest-steppe ecotone are drought-limited and thus susceptible to rising temperatures (e.g., Davi et al., 2010; Dulamsuren, Hauck & Leuschner, 2010, Dulamsuren et al., 2013; Liu, Williams, & Allen, 2013). Drought limitation was evidently predominant in this area since a long time, because the forest border in the Central Asian steppe region is located in a north-south precipitation gradient, where water shortage is the principal factor limiting tree growth (Gunin, Vostokova, Dorofeyuk, Tarasov, & Black, 1999).

The southern boreal forests in Mongolia (c. 73,800 km², Dulamsuren et al., 2016) consist mostly of stands strongly dominated by Siberian larch (*Larix sibirica* Ledeb.). Therefore, we selected monospecific *L. sibirica* forests for our study. Forest stands in the study area were subjected to industrial timber harvest in the second half of the twentieth century until 1990, but were used for unsystematic selective logging by the rural population afterward. The forest-steppe area is home to mobile pastoralists, who keep mixed herds of sheep, goats, cattle, yak, and horses on common pastures. Livestock is not much herded and animals preferentially graze on grassland, but also penetrate into the forests along the edges and further into the interior, when the forest islands are small (Lkhagvadorj, Hauck, Dulamsuren, & Tsogtbaatar, 2013b).

The dominant bedrock type in the study region is siliceous rock, including granite and metamorphic rock (e.g., schist). In addition, cover beds of eolian sand of up to several meters thickness occur upon the lower slope positions. The prevailing forest soils are Cambisols and Leptosols. The study area is located in the zone of discontinuous permafrost (Sharkhuu & Sharkhuu, 2012).

2.2 | Climate of the study region

According to weather data vailable since 1964 (temperature) and 1968 (precipitation), the climate near Tosontsengel is highly continental with long cold winters and short summers, resulting in a sub-zero mean annual air temperature of −5.8°C (July 14.8°C, January −31.2°C). Mean annual precipitation is as low as 224 mm and peaks in July. Air temperature in Tosontsengel has increased by 0.44 K per decade since the 1960s, whereas mean annual precipitation did not show any trend. In this period, monthly temperatures have increased in all months, except in December and January; the strongest increase was found from July to September. The seasonal distribution of precipitation has changed to a certain degree with a shift from autumn to spring (May).

2.3 | Study design

We selected forests of four different size classes (classes F1–F4, Table 1) in a subregion of our study area with high forest-to-grassland ratio (Figure 1) to analyze the influence of patch size on tree growth patterns. In the smallest size class, we also selected forest stands in a subregion with low forest-to-grassland ratio (class G1). Forest-dominated and grassland-dominated subregions (Fig. S1) were compared in order to analyze the influence of the degree of isolation on forest productivity and stand structure. Such influences could be mediated by differences in microclimate and land use intensity. Three replicates were studied for each plot type (F1–F4 and G1) yielding a total of 15 sampled forests. The F-type plots were selected from clusters where all four size classes were represented in order to reduce potential effects of physiographic heterogeneity within the study area. The clusters were evenly distributed over the forest-dominated subregion, while the individual forest patches of the different size classes were randomly selected within each cluster. The plots in the grassland-dominated subregion were also randomly selected among the available forest stands of the smallest size class. Selection of clusters and plots was based on remote sensing analysis of forest distribution in the study region. Forest stands that recently had changed their size class were not selected as sample plots. Plots of 20 m × 20 m were selected in the interior of each forest stand, and the geographic position was determined by GPS. Selection was by random, although moist depressions, which are not characteristic for most of the forest area, were avoided. The outermost 30 m of the forests was excluded from the plot search to avoid bias by direct edge effects. As a result from this random selection procedure, the plots were not necessarily located right in the center of the forest stands (Table 1). To account for spatial heterogeneity in the forest islands, two plots were selected per forest stand and tree ring chronologies were pooled for these subplots (Figure 2). These subplots were selected randomly within a radius of 100 m from the first randomly selected subplot, still following the rule that a minimum distance of 30 m from the nearest forest edge had to be kept.

TABLE 1 Plot types selected to study the effect of forest stand size and isolation

Class	Forest size (km²)	Forest-to-grassland ratio	Realized size (km²)	Distance to lower forest line (m)	Elevation (m a.s.l.)
F1	<0.1	High	0.04 ± 0.00	98 ± 27	1943 ± 98
F2	0.1−1.0	High	0.15 ± 0.04	173 ± 13	1923 ± 45
F3	1.1−5.0	High	2.9 ± 0.8	153 ± 42	1946 ± 46
F4	>5.0	High	30.2 ± 7.6	297 ± 20	1978 ± 42
G1	<0.1	Low	0.09 ± 0.02	82 ± 24	1981 ± 45

Arithmetic means ± SE. "Realized size" specifies the forested area of the specific stands selected for sampling in contrast to size classes ("forest size") that were used for defining the plot types.
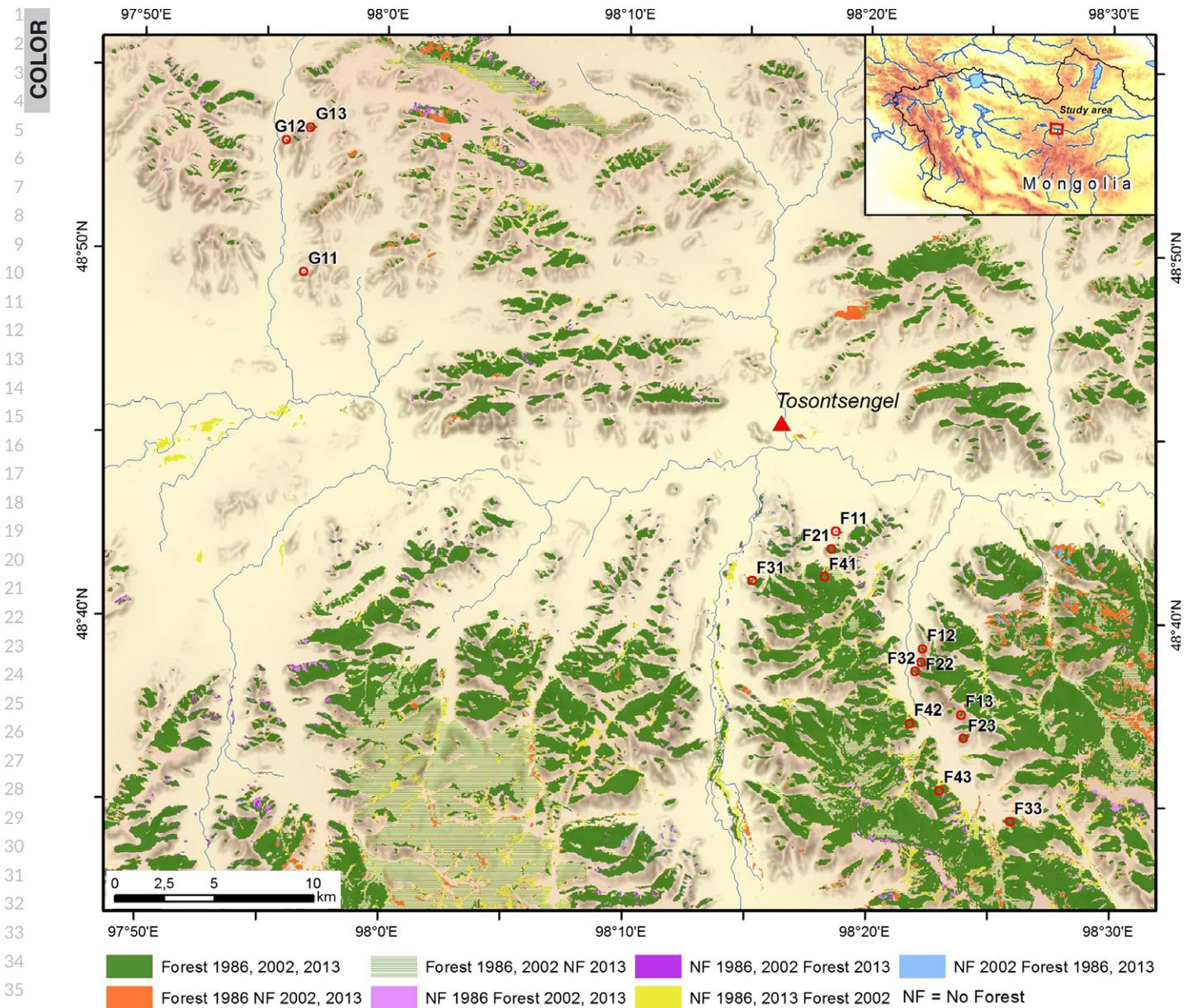
FIGURE 1 Study area near Tosontsengel, Mongolia with distribution of clusters of forest stands of different size (increasing from F1/G1 to F4) in subregions with high (F1–F4, south-eastern part of the study area) or low (G1, north-western part) forest-to-grassland ratio. Forest area changes between 1986 (Landsat 5, July 23), 2002 (Landsat 7, June 9), and 2013 (Landsat 8, September 19) are indicated by different signatures. The last digit in the stand numbers specifies plot clusters 1–3

2.4 | Structural characteristics and humus layer depth of the studied forest stands

Stand structure was studied in order to assess how well the studied stands of the different plot types were comparable in terms of basic structural characteristics. The different plot types (F1–F4, G1) did not differ significantly in their stand density (c. 1100–1880 trees/ha) and basal area (30–44 m²/ha) or in the mean (107–157 years) and maximum ages (c. 270–340 years) of *L. sibirica* trees (Duncan's multiple range; Table S1). None of the aforementioned parameters increased or decreased with stand size, except for mean tree age in the forest-dominated subregion, which showed a tendency for decrease with stand size. This trend was the result of the increasing

occurrence of young (≤60 year-old) trees with stand size; trees ≤60 years were even absent from the smallest stands (<0.1 km²) of the forest-dominated subregion (F1). Forests in the grassland-dominated subregion of the same size (G1) had high numbers of ≤60-year-old trees (Table S1). For the other tree age classes, no change in abundance with forest size was detected. The stand types did not differ significantly in the depth of the organic layer (c. 2 cm), nor of the Ah horizon (c. 7–11 cm; Table S1).

2.5 | Stand microclimate

Below-canopy microclimate was measured to characterize the temperature, humidity, and moisture conditions of independence of
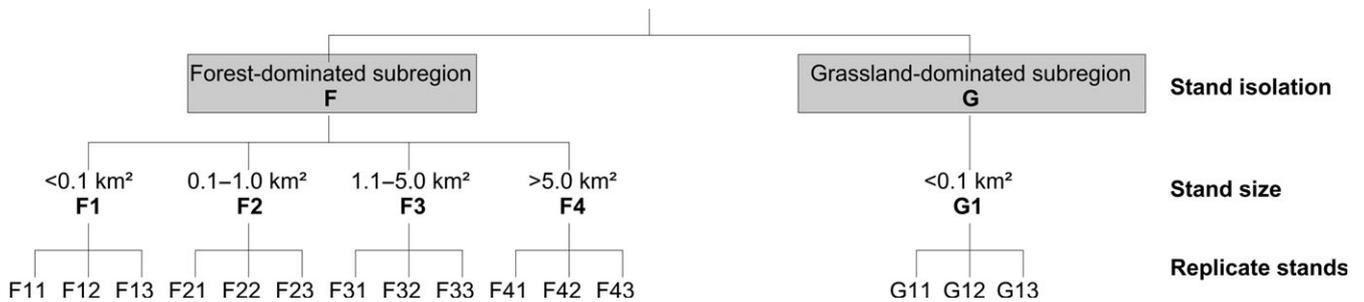
FIGURE 2 Plot design for studying the effect of stand isolation (forest-dominated vs. grassland-dominated area) and, within the forest-dominated subregion, stand size on *Larix sibirica* stands. Two plots of 20 m × 20 m were studied per replicate stand; data per stand were averaged

stand size and stand isolation. Air temperature and relative air humidity were recorded in every sample plot using HOBO U23 ProV2 sensors (Onset Computer Cooperation, Bourne, Massachusetts, USA). The sensors were placed on the northern side of three randomly selected trees at *c.* 150 cm above the ground. Temperature and relative air humidity were logged hourly for one year from August 2014 to July 2015. Soil temperature was recorded with tempmate B4 Miniature Hygrologgers (imec Messtechnik, Heilbronn, Germany) in one randomly selected plot cluster within the smallest (F1) and the largest (F4) forest stands for the same period. Sensors were placed in soil profiles at 1, 50, 100, 150, and 200 cm depth in the F1 plot and at 1, 50, 100, 125, 150, and 175 cm in the F4 plot. In the F4 plot, sensors were not installed up to 200 cm depth, because deep permafrost hampered the installation. Soil temperature was recorded twice a day at 3:00 a.m. and 3:00 p.m.

2.6 | Remote sensing analysis of forest distribution

The remote sensing analysis of forest distribution was performed with ArcGIS 3.2. The aim of the analysis was to determine stand sizes and to study the temporal dynamics of forest stand sizes to avoid that the results from tree ring analysis were influenced by recent fluctuations in stand size. The forest distribution in the study area was determined by supervised classification of a Spot 6 multispectral satellite image of September 14, 2014. The spatial resolution of this image of 1.6 m × 1.6 m enabled a detailed delineation of forest stands and isolated trees. The classification result was visually corrected and transformed into vectored data. The size of the single polygons bordering the closed forests was used to calculate the forest areas. To proof the spatial permanence of the investigated forests during the last 30 years, a change detection analysis was performed using three different Landsat satellite images: Landsat 5 TM of July 23, 1986; Landsat 7 ETM+ from June 9, 2002; Landsat 8 OLT/TIRS of September 19, 2013. Initially, the forest distribution of every satellite image was delineated by supervised classification. The computed forest areas of every time slice were subtracted from each other to analyze potential area changes. The spatial resolution of Landsat images of 30 m × 30 m induces a minor inaccuracy depending on the relative portion of trees in one pixel. Therefore,

single trees cannot be detected and the borders of closed forests can slightly alternate between the different classifications. However, closed forests are generally satisfactorily distinguished. Although there was forest disturbance by fire in the surrounding region, a significant change in forested area during the studied period can be ruled out for the investigated sites.

2.7 | Field and laboratory methods related to tree ring analysis and stand surveys

Tree ring analysis, including the analysis for the climate response of tree ring width, for missing rings and for forest regeneration, formed the central part of our study. Wood cores from all *L. sibirica* trees (1755 individuals) with a stem diameter of ≥3 cm were collected with an increment borer with an inner diameter of 5 mm at 1.3 m height above the ground. Samples were taken parallel to the contour lines of the mountain slopes to avoid compression wood. In order to use more reference samples to establish long-term tree ring chronologies, old trees growing in the neighborhood of the plots were also sampled (in total 135 trees; F1: 29, F2: 46, F3: 32, F4: 6, G1: 22 trees). These trees were included in the tree ring chronologies, but not in the analysis of age and stand structure. Only 1198 trees were included in tree age analyses, as incomplete cores (primarily due to rotten pith) had to be excluded. Additional data, such as trunk circumference, tree height, dominance (dominant, subdominant and suppressed), and fire scars, were recorded in the field. The recent regeneration of *L. sibirica* was analyzed by counting seedlings and saplings (stem diameter <3 cm at 1.3 m height, or trees not reaching 1.3 m height) of five different height classes (<50 cm, 50–100 cm, 100–150 cm, 150–200 cm, >200 cm) in the field. Stem cross sections were collected from randomly selected individuals of each size class to assess sapling age. For analyzing the effect of selective logging, tree stumps were counted. We distinguished visually between stumps remaining from logged trees and those originating from natural mortality.

Wood cores were mounted on wooden strips with grooves to hold the cores, and then, they were cut lengthwise with a microtome. The contrasts between annual tree rings were brought out with chalk. The tree ring width was measured to an accuracy of

10 μm using a Lintab 5 measuring system (Rinntech, Heidelberg, Germany). The shifts of a movable object table were electronically transmitted to a computer system equipped with Time Series Analysis and Presentation (TSAP)-WIN software (Rinntech). Stem cross sections of saplings were soaked in distilled water for one week and then cut with a sliding microtome (Hn 40, Reichert-Jung, Nußloch, Germany) into 20- to 25-μm-thick sections. Tree rings were counted on images from sections stained with safranin and alcian blue.

2.8 | Evaluation of tree ring data

Tree ring data were evaluated with the TSAP-WIN software. We classified trees into four age classes including "very old trees" (>160 years), "old trees" (101-160 years), "middle-aged trees" (61–100 years), and "young trees" (≤60 years) according to their cambial age at 1.3 m above the ground. For identifying the year of establishment, 10 years were added to cambial age. Thirty-eight percent of very old trees and 8% of old trees had rotten piths so that their year of establishment could not be determined.

Tree ring series were cross-dated to check the quality of the tree ring counts and to identify missing rings (i.e., years without stem-wood formation). Tree ring series integrated in a mean curve had to have a coefficient of agreement ("Gleichläufigkeit" [GL], Eckstein & Bauch, 1969) >65% and a (standard) t-value >3. These criteria were met by c. 90% of the samples. The applied parameters measure the similarity between tree ring series in the high- (GL) and low-frequency (t) domains, respectively. Trend lines were calculated applying five-year moving averages. Standardization of tree ring series to remove the age-dependent decline of tree ring width (Carrer & Urbinati, 2004; Helama, Lindholm, Timonen, & Eronen, 2004) was performed by applying the equation $z_i = w_i/m_i$, where z_i is the tree ring index, w_i is the tree ring width, and m_i is the 5-year moving average of year i (Dulamsuren et al. 2013). High replication on the tree level was applied to minimize the effect of stand-internal disturbances (e.g., the natural death of a neighboring tree) and stand-external disturbances (e.g., insect infestations, fire, selective logging), tree-specific characteristics resulting from genetic variation, and the effect of small-scale variation of site parameters on the tree ring index. The expressed population signal (EPS; Wigley, Briffa, & Jones, 1984) was calculated to quantify how well our tree ring series represented the stem increment dynamics of the studied stands (Table S3). The EPS was calculated separately for age classes using ARSTAN software (Cook & Holmes, 1984). Good representation by a given tree ring series is accepted at EPS >0.85.

Climate-response analysis was conducted separately for the different age classes in each patch size using monthly means of temperature and precipitation from the complete interval covered by the climate station in Tosontsengel. The strength and direction of the correlation were quantified with standardized beta coefficients. All tree ring series that could be correctly cross-dated and that were complete for the period where climate data were available were included (1,514 trees). This number included the tree ring series with missing rings. In addition to climate-response

analysis, principal component analysis (PCA) was calculated for the tree ring index in variation of monthly temperature and precipitation values.

While the tree ring index removes much of the long-term (low-frequency) variation of annual stem increment, regional growth curves (RGC) were applied to remove age-related long-term trends, but to keep all other long-term trends in annual stem increment (Sarris, Christodoukalis, & Körner, 2007; Dulamsuren, Hauck, Khishigjargal, et al. 2010). In RGC, the cumulative annual stem increment is plotted vs. age (and not the calendar year). Long-term trends that are not related to tree age are detected by comparing the stem increment between different age classes of trees at a given age.

Raw increment data over the whole lifespan of each tree were used to calculate the mean sensitivity and the autocorrelation coefficient of the tree ring series. The sensitivity is a measure for the intensity of climate signals in the tree ring series. The autocorrelation coefficient provides information of the physiological buffering capacity of trees. Mean sensitivity was calculated as the difference in the tree ring width of consecutive years divided by the mean tree ring width of the 2 years. First-order autocorrelation, which analyzes the linear correlation of tree ring width in a given year with tree ring width in the previous year, was calculated for all consecutive years of each tree ring series. High autocorrelation, despite inter-annual variations in climate, suggests that the tree is able to compensate for climatically unfavorable conditions with its stored carbohydrates.

2.9 | Statistical analyses

Arithmetic means ± standard errors are presented throughout the paper. Data were tested for normal distribution with the Shapiro–Wilk test. Multiple comparisons were made with Duncan's multiple range test. Degrees of freedom (df) for multiple tests are specified for model and error ($df_{model, error}$). These tests were computed with SAS 9.4 software (SAS Institute Inc., Cary, North Carolina, USA); linear multiple regression analyses for climate-response analysis and PCA were calculate with R software (R Development Core Team).

3 | RESULTS

3.1 | Forest size and isolation effects on microclimate

The small forest stands in the forest-dominated subregion (F1, F2), and the smallest stands (F1) in particular had a more extreme climate with higher annual amplitudes than the large forests (F3, F4). The small stands were characterized by lower minimum and higher maximum air temperatures and lower relative air humidity than the large stands (Figure 3, Table S2). As cold temperatures prevail in the Mongolian forest steppe with its short growing season, mean annual temperature was also lower in the small than in the large stands. The forest stands in the grassland-dominated subregion had lower mean, minimum, and maximum air temperatures than the forests in the forest-dominated subregion. The smallest forests in the forest-dominated subregion (F1) had lower values of relative air humidity than
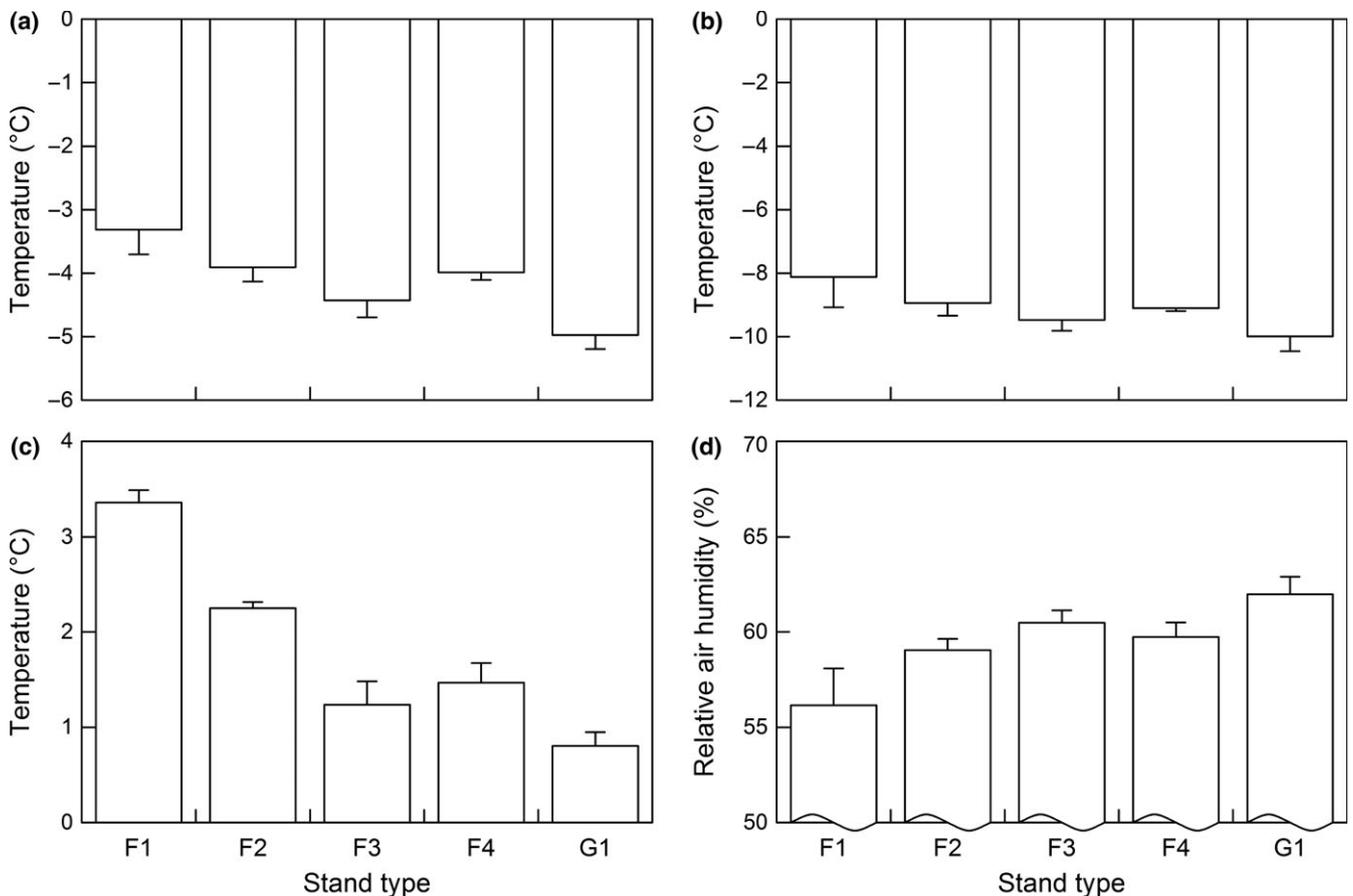
FIGURE 3 (a) Mean, (b) minimum, and (c) maximum air temperatures, and (d) relative air humidity in forest stands of different size (increasing from F1/G1 to F4) in subregions with high (F1–F4, south-eastern part of the study area) or low (G1, north-western part) forest-to-grassland ratio based on measurements from August 2014 to July 2015

all other forests (Figure 3). The forests in the grassland-dominated subregion (G1) were colder than those in the forest-dominated area (Figure 3), although there was no difference in elevation (Table S1). This difference referred primarily to maximum temperature.

Mean soil surface temperature was much lower in the small (F1: -4.1 ± 0.5°C at 1 cm depth) than in the large (F4: -2.7 ± 0.4°C) forest (Figure 4). Below 1 m depth, mean soil temperatures of the two forests became similar due to the significant temperature increase with increasing soil depth in the small forest, whereas mean soil temperature increased much less with depth in the large forest. Maximum soil temperatures sharply increased and minimum soil temperatures sharply decreased toward the surface in both forests, with the maximum and minimum temperatures in the large forest being consistently somewhat higher than in the small forest. Despite lower soil temperatures in small than in the large forests, spring melt of soil water occurred later by 6 days at 1 cm, and 33 days at 50 cm depth in the large forest (Fig. S2). The difference at 50 cm depth corresponded to a melt of soil water in mid-May (F4) instead of mid-April (F1), which was attributable to a more rapid warming of the air in the small forest in spring (data not shown). A possible explanation for this faster spring warming in the small forests could be lower snow accumulation due to higher wind exposure. In mid-

summer, ice crystals were found at much greater depth in the small (at c. 2 m depth) than in the large forest (c. 75–125 cm depth).

3.2 | Climate response of annual stem increment in variation of stand size

Mean sensitivity, first-order autocorrelation, as well as the results of the climate-response analysis of annual radial stem increment in *L. sibirica* depended on forest stand size. Mean sensitivity decreased from roughly 40% in the smallest forests to c. 30% in the largest forests in all age classes (Table 2). First-order autocorrelation increased from c. .6 to .8 in more than 100-year-old trees from small to large forests. Similar trends were also visible in less than 100-year-old trees, but were not significant.

The results of the climate-response analysis were also influenced by stand size (Table 3). Trees more than 60 years old were more sensitive to low summer precipitation and high summer temperatures in small forest stands (size classes F1–F3) than in large forests of >5 km² size (F4). These relationships mostly referred to the climatic conditions in the year prior to stemwood formation. The tree ring index in the trees of size classes F1 to F3 was mostly positively correlated with previous year's June precipitation. In the few cases,
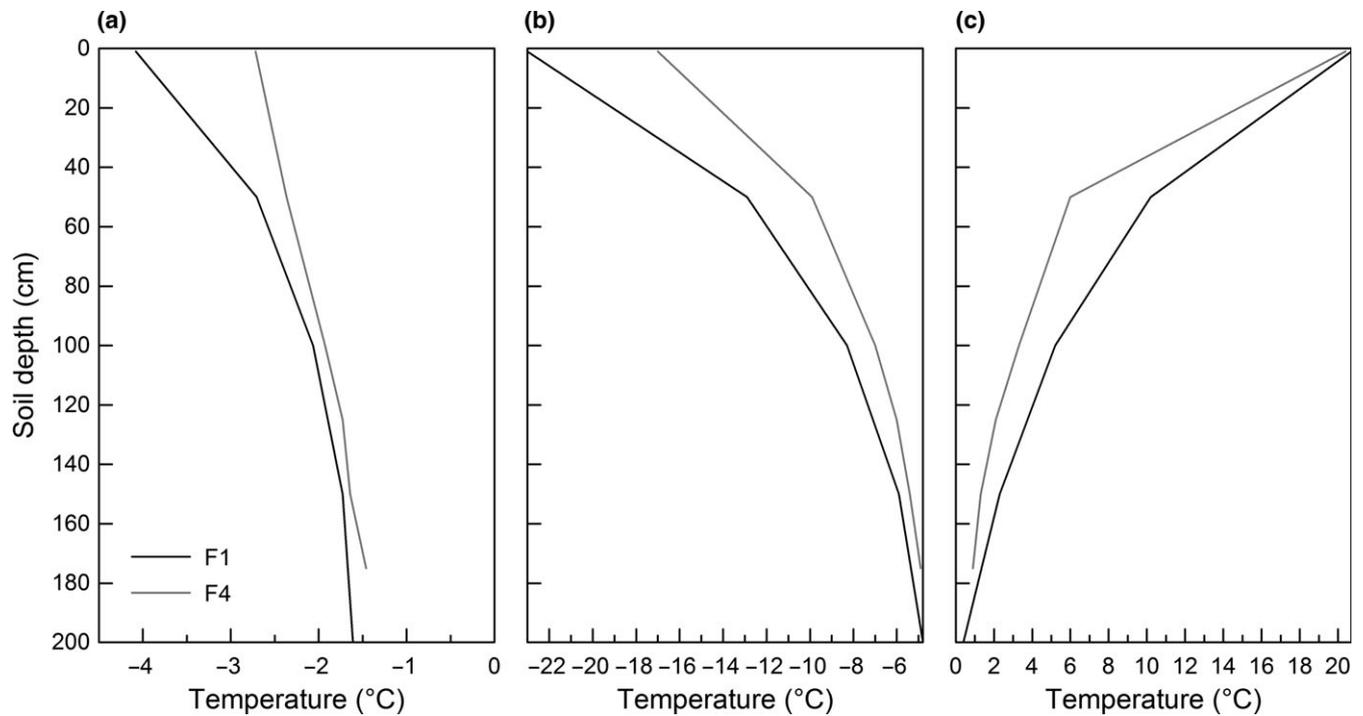
FIGURE 4 (a) Mean, (b) minimum, and (c) maximum soil temperature as a function of soil depth in <0.1 km² (F1) and >5 km² large (F4) *Larix sibirica* stands in the forested subregion based on measurements from August 2014 to July 2015.

TABLE 2 Mean sensitivity and first-order autocorrelation of tree ring width in dependence on forest stand size, isolation, and tree age

	≤60 year	61−100 year	101−160 year	≥161 year
Mean sensitivity				
F1	−	.42 ± .01 ab	.45 ± .01 a	.42 ± .01 a
F2	.38 ± .02 ab	.38 ± .01 ab	.39 ± .01 ab	.38 ± .01 ab
F3	.33 ± .02 ab	.39 ± .01 ab	.36 ± .01 ab	.35 ± .01 ab
F4	.30 ± .01 a	.31 ± .01 a	.29 ± .01 b	.32 ± .01 b
G1	.55 ± .01 b	.49 ± .01 b	.47 ± .01 a	.44 ± .01 a
Autocorrelation coefficient				
F1		.61 ± .03 a	.63 ± .01 a	.64 ± .01 a
F2	.61 ± .03 a	.71 ± .01 a	.69 ± .01 ab	.68 ± .01 a
F3	.68 ± .02 a	.74 ± .01 a	.77 ± .01 bc	.70 ± .02 a
F4	.72 ± .02 a	.79 ± .01 a	.80 ± .01 c	.82 ± .01 b
G1	.70 ± .01 a	.70 ± .01 a	.65 ± .02 ab	.70 ± .02 a

Arithmetic means ± SE. Within a column, means of mean sensitivity or autocorrelation, respectively, sharing the same letter do not differ significantly ($p \leq .05$, Duncan's multiple range test, $df_{model, error}$ = 4, 10).

where this correlation was not significant ($p \leq .05$), there were correlations that were at least marginally significant ($p \leq .10$). Several significant positive correlations were also found with previous year's August precipitation in the size classes F1–F3. In the small forests of classes F1 and F2, significant increases of the tree ring index occurred with decreasing July temperature of the year before tree ring formation were detected in a few cases. The summer climate of

the current year was much less influential. Young trees (≤60 years) showed different and less consistent responses to temperature and precipitation.

Promotion of stem increment by the previous year's summer precipitation was also suggested by PCA (Figure 5). June and August precipitation of the previous year explained ≥70% of the variation of the tree ring index. Stand types were increasingly associated with high values of precipitation with decreasing stand size.

3.3 | Effect of forest stand isolation on the climate response of annual stem increment

Forest-to-grassland ratio had no significant effect on mean sensitivity and first-order autocorrelation (Table 2). The former was similarly high and the latter as low in the G1 as in the F1 plots. Annual stem increment in the trees from G1 plots increased with increasing summer precipitation of the year prior to tree ring formation (Table 3). In contrast to the F1 plots, this increase was not limited to June and August, but also concerned the most precipitation-rich month July, at least in trees that were more than 100 years old. PCA results suggested that the tree ring index in the G1 plots was associated even more strongly with high summer precipitation than in the F1 (and any other F) plots.

3.4 | Variation of tree ring width

The interannual variation of annual radial stem increment showed high synchronicity across the different locations as evidenced by the

TABLE 3 Response of the tree ring index of *Larix sibirica* trees of different age groups to monthly temperature and precipitation of the year of and the year prior to tree ring formation

	Temperature											Precipitation											
	Prior year						Current year					Prior year							Current year				
	3	4	5	7	8	12	1	2	3	5	8	3	4	5	6	7	8	11	3	4	5	6	7
F1																							
VO															●		●					●	
O											●		○				●	○				○	
M				■							●				●		●	○		●			
Y																							
F2																							
VO													○		○	○						●	
O				■							●				●		●			●			
M				■	●						●	□			●		●	○		●			
Y							■	○		●							○	●		●		○	
F3																							
VO										○					●		●						
O		□													●			○				○	
M												□	○		●		●						
Y				○					■	○					○		○	○				○	□
F4																							
VO									□								○						
O												□					○						
M						□																	
Y			○				□	●	□						○		●						
G1																							
VO	●					□								○	○	●	●		●				
O	●			□		■									●	●	●		●				
M															○	●	●						
Y		○			□	□	□	□	□	□	□	□	○	□	□		●	□			□		□

Correlation significant (*p* ≤ .05): ● positive, ■ negative correlation; marginally significant (*p* ≤ .10): ○ positive, □ negative correlation. Months are identified with numbers 1 to 12. Forest stands increasing in size (from F1/G1 to F4) in the forest (F)- and grassland (G)-dominated subregions. VO, very old trees (>160 years); O, old trees (101–160 years); M, middle-aged trees (30–100 years); Y, young trees (<60 years).

largely parallel variation of the tree ring indices in trees from forests of different size and degree of isolation (Figs S3, S4). Calculated for a long period (1900–2014) mean tree ring width amounted to 0.3–0.4 mm and did not significantly differ between forest stand types. However, tree ring width differed between the large forests of >5 km² (F4) and the smaller forest stands (F1–F3) in individual periods (Figure 6). These data in Figure 6 are displayed for different age classes to reduce effects of age-dependent growth variation. From the late eighteenth to the mid twentieth century, trees of stand type F1–F4 mostly shared the same positive and negative peaks in annual tree ring width, but at different amplitudes. Mean tree ring width reached far higher values in periods of favorable growth conditions in small forests (F1–F3) than in large forests, but was on a similar scale during intervals with slow growth. Since the late twentieth century, however, mean tree ring width in the large forests of >5 km² (F4) exceeded that in the smaller forests for up to 160-year-old trees (Figure 6). Very old trees (>160 years of cambial age) showed similar stem increment across the differently sized stands in recent time, but had repeated pulses of higher increment in the <5 km²-sized forest than in the larger forests before (Figure 6d).

Cumulative RGC revealed that middle-aged trees (cambial age 61–100 years) grew faster in recent decades than old trees (101–160 years) did in the past at younger age in the F1 plots, but not in the other forests (Fig. S5). Middle-age trees in the small forests (F1, F2, G1) and all trees in the largest forests (F4) recently showed an upward curvature in the graph for cumulative stem increment indicating growth releases.

3.5 | Missing ring frequency

From 1900 to 2014, annual mean frequency of missing rings (Table 4) was lower in the forests of >5 km² size (F4) than in the smaller forests (F1–F3, G1). There was a marked increase in
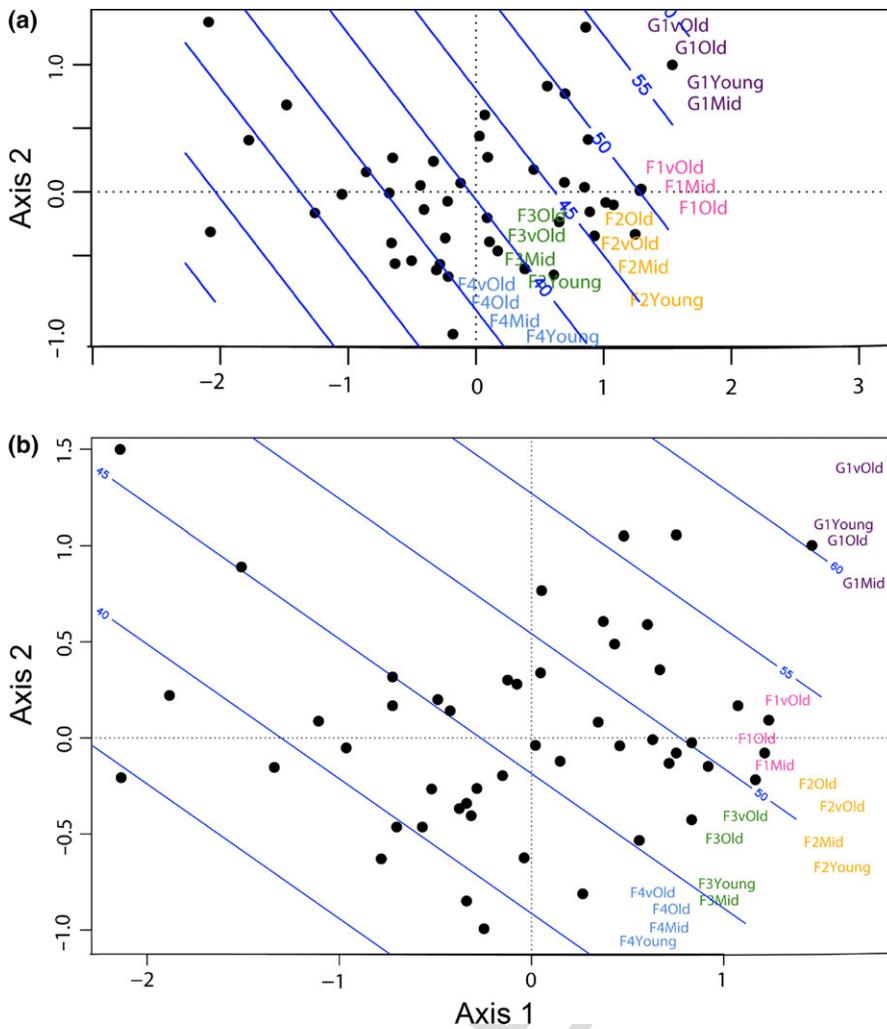
FIGURE 5 PCA for the tree ring index of *Larix sibirica* saplings in stands of increasing size (from F1/G1 to F4) in the forest (F)- and grassland (G)-dominated subregions in variation of (a) June and (b) August precipitation of the previous year. Dots represent individual years from 1964 to 2014, and contour lines represent levels of precipitation. Explained variance: (a) 72% (axis 1), 8% (axis 2); (b) 70% (axis 1), 9 (axis 2). Total variance: (a) 40.45, (b) 38.59.

missing ring frequency after 1970 in all forests of <5 km² size. Frequency increased by the factor 2.4–3.3 in the larch stands of the forest-dominated subregion (F1–F3), but by the factor 7.9 in the grassland-dominated subregion (G1). In contrast, the large forests of >5 km² size in the forest-dominated subregion showed only a slight (insignificant) increase in missing ring frequency by the factor 1.2.

3.6 | Forest regeneration and tree stump density

Forest regeneration increased with stand size (Figure 7). The large forests of >5 km² size (F4) exhibited considerably higher sapling densities than the smaller forests (F1–F3, G1). In the F1 plots, no seedlings and saplings were found at all, whereas few saplings occurred in the small forest patches in the grassland-dominated subregion (G1).

A trend toward increasing frequency of downed tree trunks with stand size was not significant due to high variation between plots of the same stand class (Fig. S6a, b). While downed deadwood was absent from the smallest forests (F1, G1), there were 133 ± 46 downed tree trunks per ha in the largest forest stands (F4). The density of tree stumps did not differ between the stand types

(Fig. S6c). However, there was an insignificant trend to higher stump-to-live-tree ratios in the smallest (F1, G1) compared to the larger forest stands (Fig. S6d).

4 | DISCUSSION

Our results suggest that small forest stand size increases the sensitivity of annual stem increment to climate warming in the studied *L. sibirica* stands at the southern fringe of the boreal forest in the Mongolian forest-steppe ecotone. In agreement with our first hypothesis, mean sensitivity of tree ring width increased with decreasing stand size, whereas first-order autocorrelation decreased. These opposing trends give evidence of the trees' apparently reduced capacity to withstand unfavorable weather conditions and maintain the photosynthetic activity of the canopy with negative consequences for stemwood production in small forest stands. Positive correlation between the tree ring index and summer precipitation in small- and medium-sized forests of <5 km² size (size classes F1–F3), but not in large forest stands of >5 km², suggests that more intense drought exposure is indeed the cause of the higher climate sensitivity of stemwood production in small forests. A likely causal
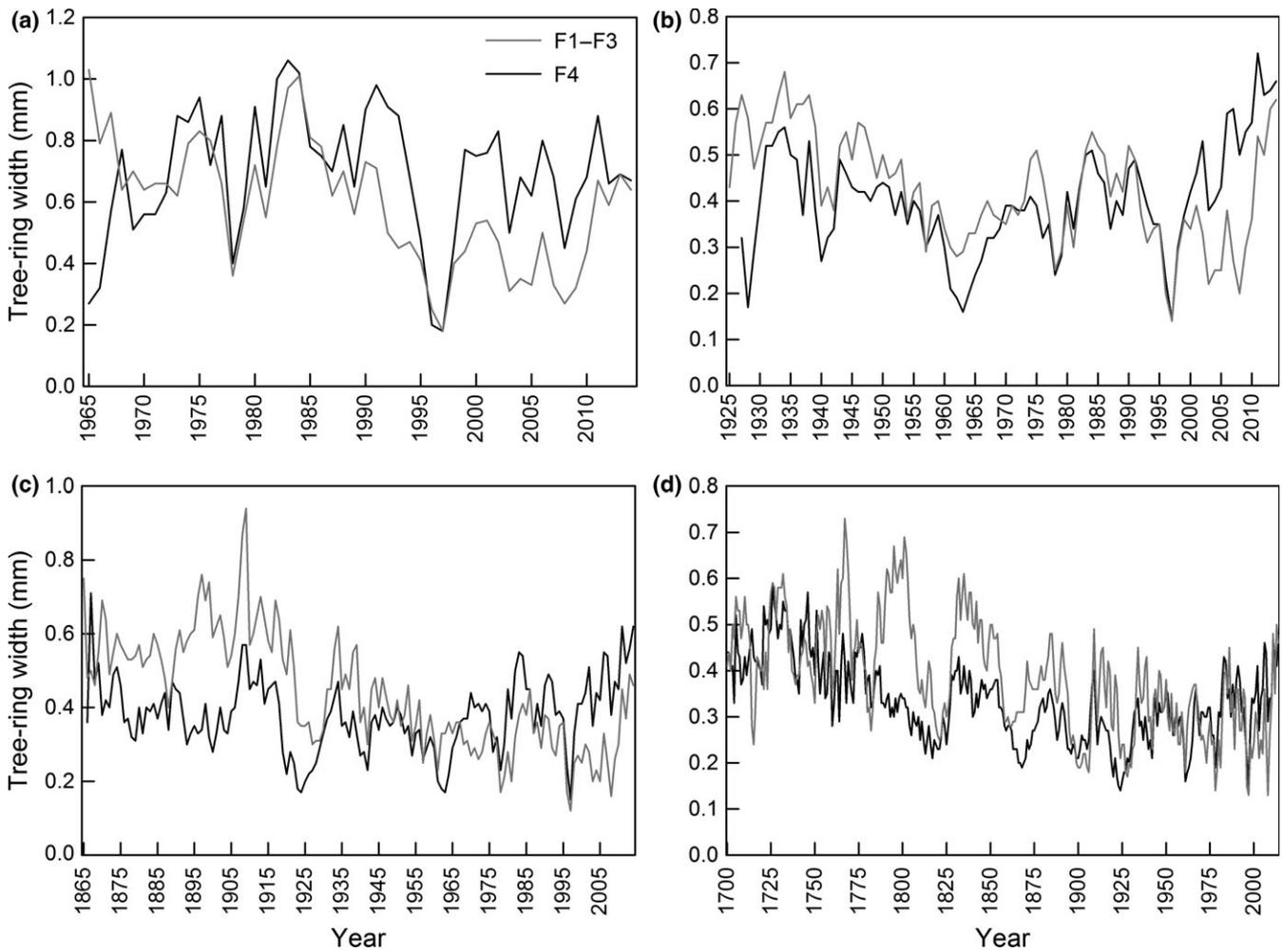
FIGURE 6 Mean tree ring width in *Larix sibirica* trees from forest stands of >5 vs. <5 km² size (stand type F4 vs. F1–F3) in the forest-dominated subregion in trees of a cambial age of (a) ≤60 years, (b) 61–100 years, (c) 101–160 years, and (d) >160 years. Note different scale on the y-axis. Number of samples (F4; F1–F3): (a) 99; 44; (b) 56; 171; (c) 67; 425; (d) 72; 327 trees

TABLE 4 Missing ring frequency (in %) in *Larix sibirica* trees from stands of different size (increasing from F1 to F4) in subregions with high (F1 to F4) or low (G1) forest-to-grassland ratio before and after 1970

Class	1900–1969	1970–2014	Increase
F1	1.31 ± 0.14	3.96 ± 0.44*	302%
F2	1.21 ± 0.89	2.87 ± 0.37*	237%
F3	1.23 ± 0.15	4.00 ± 0.41*	325%
F4	0.87 ± 0.12	1.04 ± 0.14	120%
G1	0.71 ± 0.13	5.60 ± 1.01*	789%

Arithmetic means ± SE.
*Indicate significant difference between periods ($p \leq .05$, U-test).

chain is drought-induced reduction of stomatal conductance and resulting reduction in carbon assimilation (Dulamsuren et al., 2009). Our measurements of temperature and relative humidity, demonstrating both more extreme maximum and minimum temperatures and reduced humidity in the small forest stands, indicate that the
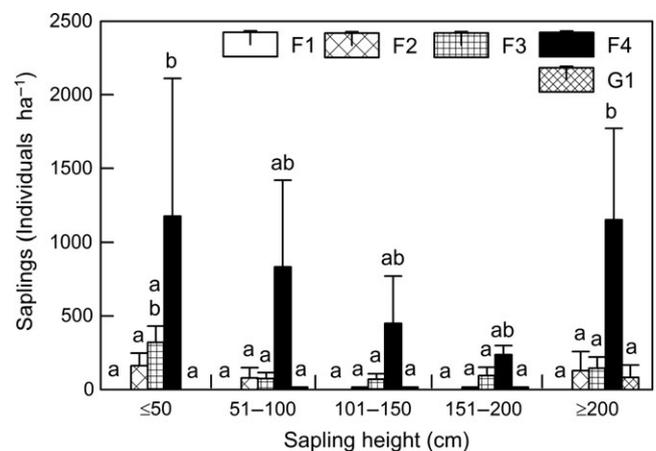

FIGURE 7 Density of *Larix sibirica* saplings in stands of increasing size (from F1/G1 to F4) in the forest (F)- and grassland (G)-dominated subregions. Means (±SE) sharing a common letter do not differ significantly ($p \leq .05$, Duncan's multiple range test, $df_{model, error} = 23, 51$).

small forests were drier and warmer in summer than the large stands. A warmer and drier summer microclimate in forest fragments has repeatedly been reported from woodland regions around the world and has been attributed to edge effects. The smaller the forest patch, the larger is the proportion of the forest's interior area that is influenced by the microclimate of the open land in the surroundings (Chen et al., 1995).

While the edge effect causes higher mean temperatures inside small forest patches in subtropical to warm-temperate regions (Saunders et al., 1991), higher maximum and lower minimum temperatures in the cold-temperate high-elevation forest steppe of Mongolia result in a reduction of mean annual temperature with decreasing forest size. This pattern is attributable to the long winter in Mongolia's forest-steppe region, which largely determines mean annual temperature that lies below freezing point in many regions of the country (Hauck, Dulamsuren, & Leuschner, 2016). The generally lower temperatures in the grassland-dominated forest steppe compared to the forest-dominated landscape may result from higher wind speeds (Kelliher, Leuning, & Schulze, 1993) and from the higher albedo of grasslands than of boreal forests especially in winter (Li et al., 2015; Helbig et al., 2016). Furthermore, the higher aerodynamical roughness of forests compared to grasslands causes a greater potential to heat the air (Baldocchi & Vogel, 1997). Lee, Goulden, and Hollinger (2011) quantified the warming effect of forests for the boreal forest biome north of 45°N as to be 0.85 K for mean air temperature. The forest-to-grassland ratio has primarily an effect on maximum temperatures, which contrasts with the effect of forest size on the microclimate. Although the effect of forest vs. grassland vegetation on microclimate is undisputed, spatial microclimatic variation due differences in micro-topography, of course, also influences forest distribution by excluding trees from dry and hot sites.

The cooling effect of reduced forest stand size during winter can also explain the higher mean and minimum soil temperatures recorded in large (F4) as compared to small (F1) forests. This stand size effect apparently caused deeper freezing in the permafrost soil of the small forests compared to the large forests, a result which might contradict intuitive expectations, but which is in agreement with more frequent frost events at the edge than in the interior of forests as postulated by Geiger (1965) and Saunders et al. (1991). While stand-replacing disturbance by clear-cut or fire is widely reported to deteriorate permafrost (Jin et al., 2007), forest fragmentation without alteration of forest cover, as was studied by us in the Mongolian forest steppe, apparently does at least not completely destruct the permafrost in the forest islands. Our microclimate measurements refer to below-canopy climate and are, thus, relevant to permafrost conditions, but differ from the microclimate above and within the microclimate (Pomeroy & Dion, 1996; Baldocchi & Vogel, 1997), which is more influential on the trees' stomatal conductance. Differences in organic layer thickness were not found between stand types and thus could not have contributed to the variation in soil temperature.

A two to threefold increase in missing ring frequency in the forest <5 km² size (F1–F3), but not in the forests >5 km² (F4), since the 1970s is in line with the greater climate sensitivity of the trees in small forests. Missing rings are induced by drought during the growing season (Lorimer, Dahir, & Singer, 1999; Khishigjargal et al., 2014; Liang, Leuschner, Dulamsuren, Wagner, & Hauck, 2016). The absence of a trend for increased frequency of missing rings with late twentieth century warming in the large forests thus suggests less tense water relations than in the small forests. This result matches with the absence of significant correlations of mature tree's stem increment with summer precipitation and temperature in large forests. While climate sensitivity increased gradually with decreasing forest size, the dependence of missing ring frequency on stand size was nonlinear, with low frequency only in large continuous forests (F4). Our second hypothesis supposing a gradual change of missing ring frequency with forest size was thus not fully supported. It has been shown that missing ring frequency is in general not dependent on tree age (Lorimer et al., 1999), suggesting that the recently increased occurrence of missing rings in the forests of <5 km² was not an effect of potential changes in stand age structure over time.

Forest regeneration increased with stand size in agreement with our third hypothesis. It is plausible to assume that this is due to a combined effect of higher moisture availability and much lower grazing pressure in the interior of large forests than in small stands. Seed germination and seedling establishment of *L. sibirica* in the forest-steppe ecotone are known to benefit from low soil temperature and high soil moisture (Dulamsuren, Hauck, & Mühlenberg, 2008), while light seems to be of minor importance. Grazing livestock, albeit beneficial for the initial establishment of seedlings owing to the reduction of competition by the ground vegetation, is strongly limiting for sapling survival, as larch saplings are a preferred diet of cashmere goats (Khishigjargal et al., 2013). Goats avoid the interior of large forests, but are regularly found at forest edges and in the interior of small forest patches surrounded by grassland. Both climate and livestock densities have become more unfavorable for the regeneration of *L. sibirica* in the recent past, since climate has become warmer (Dagvadorj, Natsagdorj, Dorjpurev, & Namkhainyam, 2009) and the number of goats has more than tripled since the early 1990s (Lkhagvadorj et al., 2013b).

Missing ring frequency was also influenced by the isolation of the forest stands. The small forest stands in the grassland-dominated landscape (G1) exhibited a nearly eightfold increase in missing ring frequency since the 1970s. This increase was far higher than in forests of the same size (F1) in the forest-dominated landscape. Positive correlation of annual stem increment with the previous year's June, July, and August precipitation in the G1 forests, but only with June and August precipitation in the F1 (and F2, and F3) forests, is in line with the large increase in missing ring frequency. These findings, which support our fourth hypothesis, suggest that trees in the grassland-dominated forest steppe suffered from more intense drought stress than trees in the forest-dominated subregion, irrespective of forest size. Unfortunately, we do not have physiological data that would corroborate this assumption. As mean temperatures were even lower in the G1 than the F1 plots, we can only speculate that higher wind speeds in the open grassland-dominated landscape

(not measured) caused higher evapotranspiration rates than in the landscape with more forest area. Detailed measurements of microclimate variability and permafrost distribution in forest-steppe regions of variable forest-grassland ratios would be needed to interpret the observed differences in the trees' climate warming response.

An interesting detail of our results emerges from the comparison of mean tree ring widths of larch trees growing in forests of either less than or more than 5 km² size (Figure 6). Trees in the large stands (F4) grew recently faster than trees in small forests (F1–F3), whereas the opposite trend was visible in the preceding 200 years. We hypothesize that this recent switch could be due to intensified permafrost melt in large forests. The active layer was located at lower depth in the soil profile and reached higher temperatures in the large than in the small forests during summer, when melted permafrost is most critical for the water supply of the vegetation (Sugimoto et al., 2003; Lopez et al., 2010).

Our results strongly support our initial assumption that both forest size and isolation are important determinants of the climate warming response of *L. sibirica* trees in the forest-steppe ecotone. Nevertheless, there are other factors that were not investigated in this study, which likely interfere with the relationship between forest fragmentation and warming sensitivity. Major disturbances such as fire, insect calamities, and logging cause strong changes in stand structure, microclimate, and permafrost distribution (Gromtsev, 2002; Zyryanova et al., 2007) and are thus likely to affect the sensitivity of forests to climate warming. Although we have no systematic data of forest fires from our sample plots, it was obvious during field work that fire had not been restricted to small forest patches, but even had occurred in the large forests, which are more often visited by people for the collection of berries and pine nuts. Selective logging as is commonly practiced in Mongolia leads to reduced stand density, which improves the water supply of the remaining trees (Dulamsuren, Hauck & Leuschner, 2010; Chenlemuge et al., 2015) and thus should increase their tolerance to drought episodes. Clear-cuts and large forest fires, however, cause permafrost melt with a transient increase, but long-term decrease, of soil moisture (Yoshikawa, Bolton, Romanovsky, Fukuda, & Hinzman, 2003). We tried to control for these factors as much as possible in our investigation by clustering the stands of different size in our sampling design. Selective logging is usually more intense in small forests than in the interior of large forest stands in the Mongolian forest steppe (Dulamsuren et al., 2014). Logging should therefore have had a more positive effect on tree water relations in the small stands than in the large forests. As we found a stronger response to climate warming in small forests, it is not likely that logging had a decisive impact on the observed differences in climate warming sensitivity in our study. This conclusion is supported by the fact that stand density, basal area, and tree stump frequency did not differ significantly between the plot types, although there was an insignificant trend for higher stump-to-live tree ratios in the smallest forests (F1, G1) than in the other stands.

Our findings suggest that the progressive fragmentation of the southern boreal forest in the Inner Asian forest steppe due to the combined effect of logging, fire, and forest grazing (Erdenechuluun, 2006; Hansen et al., 2013) reinforces the sensitivity of the remaining forest to climate warming. The southern fringe of the boreal forest in Inner Asia is one of the world's regions with most intense climate warming (IPCC, 2013) and is already a key region of global warming-related decline of forest health (Dulamsuren, Hauck & Leuschner, 2010, Dulamsuren et al., 2013; Liu et al., 2013). The same is true for oroboreal coniferous forests south of the continuous boreal forest belt in Inner Asia (Liang et al., 2016). The potential negative impact of forest fragmentation on the climate warming tolerance of these forests has not been addressed in the literature so far. It is likely that negative feedbacks of forest size and forest stand isolation on the climate warming tolerance of forests are common in drought-limited forest ecosystems around the world. Today, these forests are suffering from drought-induced forest mortality in many regions on earth. While this process has received considerable attention (Allen, Macalady, & Chenchouni, 2010), the interaction of other factors with the tolerance of these forests to climate warming is not sufficiently studied.

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We examined the influence of stand size and stand isolation on the growth performance of larch in forests of four different size classes located in a woodland-dominated forest-steppe area and small forest patches in a grassland-dominated area. We found increasing climate sensitivity and decreasing first-order autocorrelation of annual stemwood increment with decreasing stand size. Stemwood increment increased with previous year's June and August precipitation in the three smallest forest size classes, but not in the largest forests.

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