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## SUPPLEMENTARY MATERIALS

[www.sciencemag.org/content/352/6292/1449/suppl/DC1](http://www.sciencemag.org/content/352/6292/1449/suppl/DC1)  
 Materials and Methods

Figs. S1 to S5  
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 References (27–47)

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## FOREST ECOLOGY

# Northeastern North America as a potential refugium for boreal forests in a warming climate

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High precipitation in boreal northeastern North America could help forests withstand the expected temperature-driven increase in evaporative demand, but definitive evidence is lacking. Using a network of tree-ring collections from 16,450 stands across 583,000 km<sup>2</sup> of boreal forests in Québec, Canada, we observe a latitudinal shift in the correlation of black spruce growth with temperature and reduced precipitation, from negative south of 49°N to largely positive to the north of that latitude. Our results suggest that the positive effect of a warmer climate on growth rates and growing season length north of 49°N outweighs the potential negative effect of lower water availability. Unlike the central and western portions of the continent's boreal forest, northeastern North America may act as a climatic refugium in a warmer climate.

The boreal forest biome is responsible for ~20% of the total carbon (C) sequestered annually by forest ecosystems (1) and contains a large fraction of the planet's remaining unmanaged forests (2). Over the current century, this ecosystem is expected to undergo one of the largest increases in temperatures (3). Low mean annual temperatures (MATs) are a major constraint on boreal forest productivity, and increases in temperature and growing season length in recent decades are reported to have benefited tree growth over large areas of Fennoscandia (4) and Russia (5). In central and western areas of North American boreal forests, however, anal-

ysis of recent tree-ring width data (6, 7), in combination with stable carbon isotope analysis (8, 9) and satellite images (10), suggests that changes in soil water balance have canceled potential gains in forest growth from recent warming. An increase in water deficit in these regions is suggested to have increased tree mortality in recent decades (11).

The boreal forest of northeastern North America (NENA) receives more than twice the mean annual precipitation (MAP) as its central and western counterparts, typically exceeding the mean annual evapotranspiration demand (MAE). This pattern results in a strong west-east gradient in water availability (Fig. 1A), which should continue in the future, because climate projections suggest that NENA could be the only area across the circumboreal forest with sufficient precipitation to fully compensate for increasing evaporative stress induced by warmer temperatures (2). Future increases in temperature combined with an earlier snowmelt, leading to an earlier start to the growing season, could thus allow local tree species of NENA to better withstand and even thrive in a warmer climate. Although satellite-driven measures generally support this hypothesis for NENA (12, 13), empirical studies and climate-growth models have not yet reached a consensus (14–18), and definitive evidence from well-replicated

large-scale tree growth data is lacking. Should water availability become a chronic factor limiting tree growth and survival across much of the boreal forest, NENA could act as a climatic refugium in the near future for black spruce [*Picea mariana* (Mill.) B.S.P.], the most abundant tree species throughout the North American boreal forest (19), including our study region (fig. S1).

Using a network of tree-ring collections from 16,450 stands representing much of the boreal forest east of 80°W (Fig. 1B), our objective was to determine how water availability and air temperature control interannual variations in the growth of black spruce (20). To do so, we used bootstrapped correlations to measure the influence of seasonal climate on radial growth for the period 1960–2004. Should the dominant climatic constraint on growth be low water availability, growth should be positively correlated with precipitation and soil moisture and, because evaporative demand increases with temperature, negatively correlated with temperature. In contrast, opposite results would support the hypothesis that low temperatures are the dominant climatic growth constraint. By determining the climatic sensitivity of the annual growth of 26,697 trees across a 583,000-km<sup>2</sup> area in boreal NENA, we had the potential to resolve the discrepancy between empirical studies and model forecasts on the fate of these forests under anthropogenic climate change. To this end, individual tree-ring series were standardized to emphasize interannual variations due to climatic variables and were averaged according to landscape unit and soil type (Fig. 1C).

Two strikingly different types of tree growth response to seasonal climate were detected by bootstrapped correlations (Fig. 2). The first response, dominant across the northern part of the study area, indicates that an increase in temperature with a concomitant reduction in available water has positive effects on growth. The second response, more frequent in forests south of 49°N, indicates that an increase in water availability rather than temperature has a positive effect on growth.

Support for the low-temperature constraint hypothesis is observed in summer (July and August), winter (November to April), and to a lesser extent prior-year fall (September and October) (Fig. 2). Out of the 109 chronologies, hereafter called forests, which display significant growth correlations

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( $P < 0.05$ ) with summer climate, a majority (92%), distributed at all latitudes, correlate either positively with temperature, negatively with precipitation, or negatively with a soil moisture index (SMI). Exceptions are concentrated around the Gaspé Peninsula on the south shore of the Saint Lawrence River and in southwestern Québec, where these regions have higher summer temperatures or lower precipitation than other sites at a similar latitude (fig. S2). Significant growth correlations with winter temperatures are positive in 54 out of 57 forests (Fig. 2). Finally, 18 out of 19 significant growth correlations with prior-fall temperatures are positive.

On the other hand, low water availability during the prior-year summer constrains growth, because 107 of the 109 forests with significant growth correlations with climate displayed either negative correlations with prior-summer temperature or positive correlations with prior-summer precipitation and SMI (Fig. 2). It should be noted that the contradictory patterns reported for current-year and prior-year summer are only observed in 8% of the same forests.

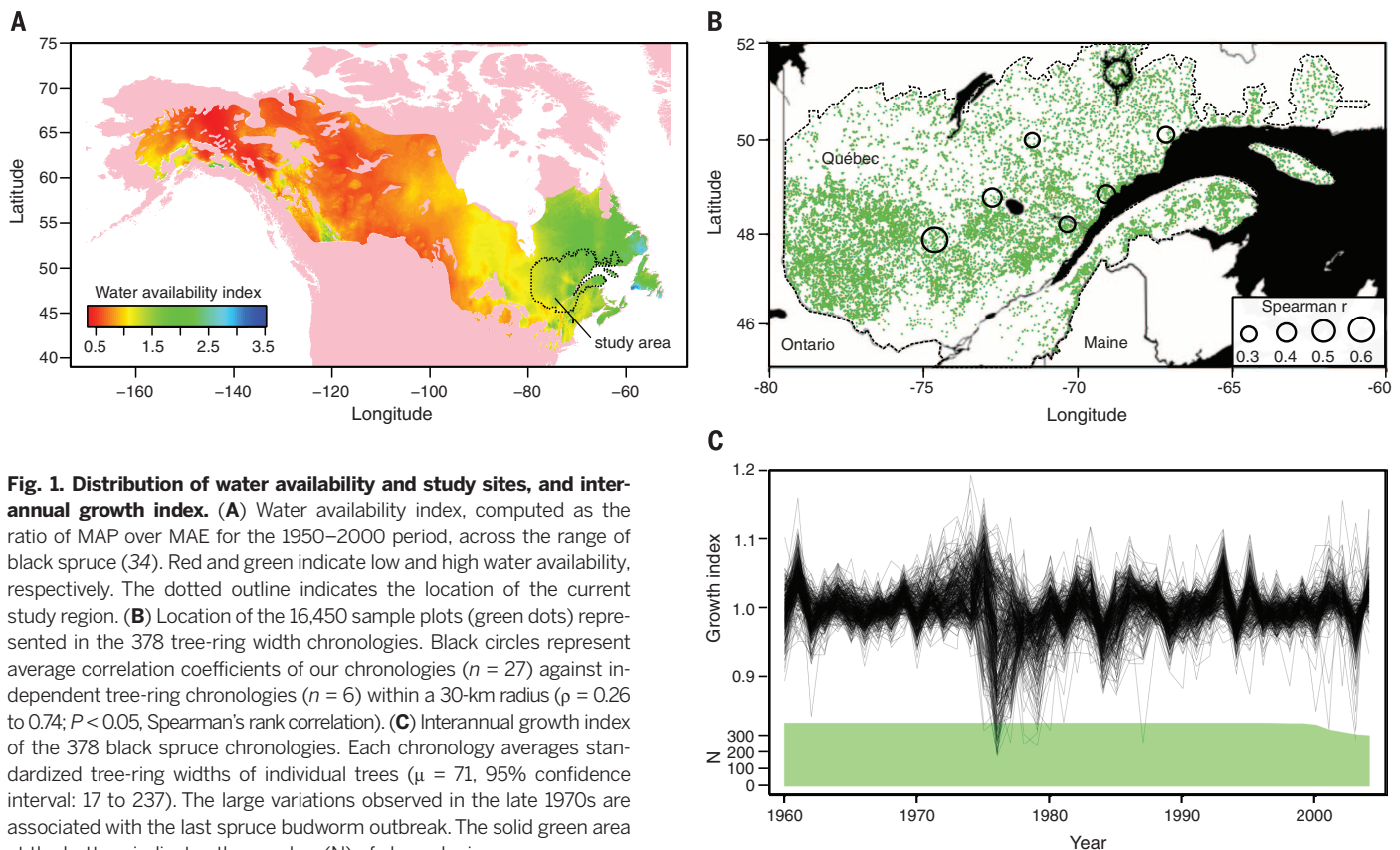
Current-summer temperature has the highest number of significant correlations with growth (67), 97% of which are positive. This largely positive trend is intuitive, given that the temperature of high-latitude forests typically limits growth rates. Across seasons, however, a majority of significant correlations with growth (76%) are related to spring, summer, fall, or winter climate before wood formation (Fig. 2). These correlations consist in lagged effects, which are common in boreal forests of

North America and Europe (16, 21). High winter snowfall has been reported to delay the spring onset of growth in Eurasia (22), which is a primary driver of the productivity of boreal forests (23, 24). In turn, spring snowmelt controls soil water saturation and temperature (25). That is, an early snowmelt hastens the drainage of excess water and allows soils to warm up faster at the beginning of the growing season. These processes have positive effects on black spruce growth (26, 27). The large-scale positive growth response to drier springs and low soil moisture for the areas north of 49°N supports these mechanisms. Reduced spring precipitation could also have benefited tree growth indirectly by being associated with higher solar radiation, which has been observed to limit photosynthesis in mature black spruce forests (24). At high latitudes, spring precipitation may still include some snowfall, because spring snowmelt averaged over 1960–2004 was completed by May 29 at the northern margin of the study area. Thus, the winter mechanisms mentioned above may also occur in the spring.

The positive growth response to high winter temperatures observed over the entire study area has been previously reported for black spruce (15) and other conifers at the northern margin of their distribution in the northeastern United States (28). It is probably associated with a reduction in winter desiccation injuries (29). Prior-year climate also influences growth in various ways: Significant amounts of nonstructural carbohydrates (NSCs) created in prior years are used for growth (30);

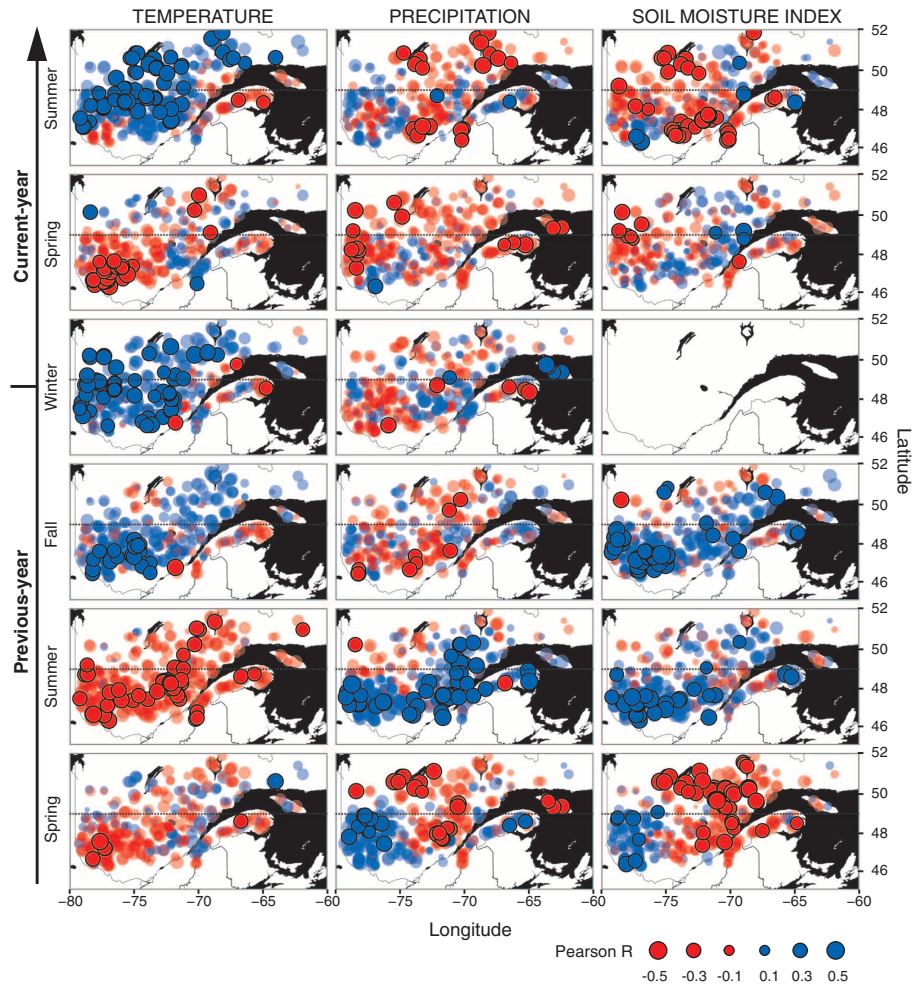
weather conditions toward the end of the growing season can stimulate water recharge in trees, a prerequisite to the following spring growth onset (31, 32); and black spruce buds formed during the previous growing season already contain a determined number of needle primordia, which will have a determinant effect on leaf area, transpiration, photosynthetic capacity, and ultimately growth. Our results support prior work underscoring the importance of all seasons when forecasting the boreal forest response to climate change (17).

From our broadly distributed network, clear spatial patterns in climatic sensitivity indicate that high temperatures and low water availability primarily constrain growth south of 49°N. Below 49°N, we find 95% ( $n = 18$  forests) of all significant positive correlations with precipitation or SMI during prior-year spring (May to June), 91% ( $n = 33$  forests) of all significant negative correlations with temperature over the current spring, and 87 to 93% ( $n = 27$  to 47 forests) of all significant positive correlations with soil moisture during prior-year summer and fall (Fig. 2). Many of these correlations are observed in the southwestern region, which combines the lowest MAP with the highest MAT of the study area (fig. S2). The latitudinal thermal gradient (Fig. 3A) and its effect on water availability thus exert a strong control on the direction of the correlation of growth with climatic variables. Combined across seasons, the majority of significant growth correlations with temperature become positive at 48° to 51°N (Fig. 3B). The majority of significant

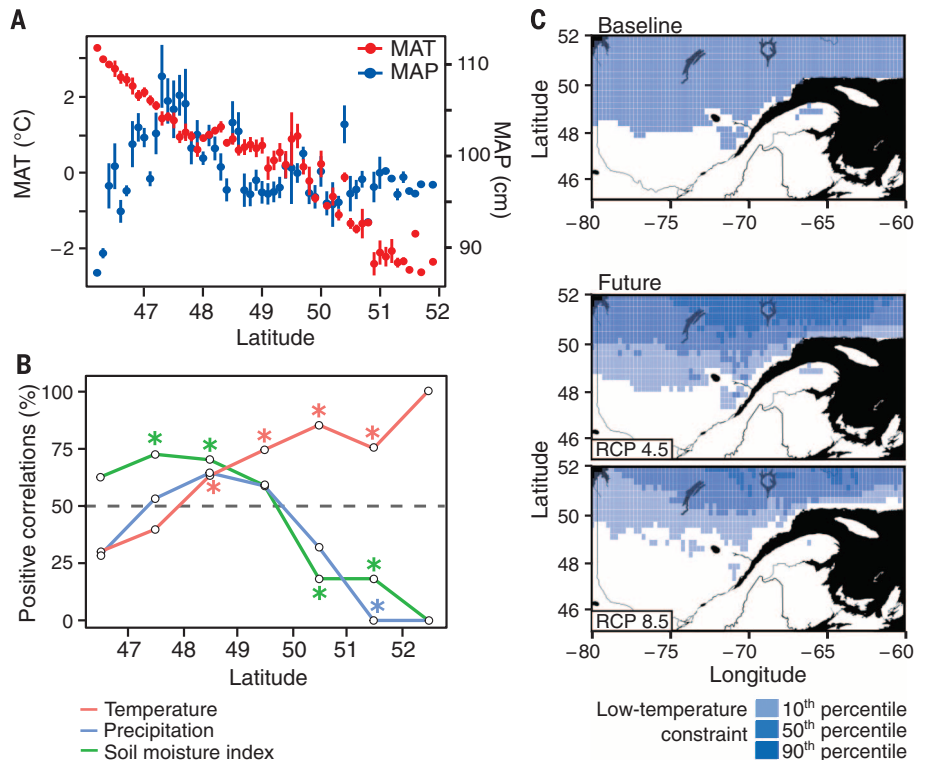


**Fig. 1. Distribution of water availability and study sites, and inter-annual growth index.** (A) Water availability index, computed as the ratio of MAP over MAE for the 1950–2000 period, across the range of black spruce (34). Red and green indicate low and high water availability, respectively. The dotted outline indicates the location of the current study region. (B) Location of the 16,450 sample plots (green dots) represented in the 378 tree-ring width chronologies. Black circles represent average correlation coefficients of our chronologies ( $n = 27$ ) against independent tree-ring chronologies ( $n = 6$ ) within a 30-km radius ( $\rho = 0.26$  to 0.74;  $P < 0.05$ , Spearman's rank correlation). (C) Inter-annual growth index of the 378 black spruce chronologies. Each chronology averages standardized tree-ring widths of individual trees ( $\mu = 71$ , 95% confidence interval: 17 to 237). The large variations observed in the late 1970s are associated with the last spruce budworm outbreak. The solid green area at the bottom indicates the number (N) of chronologies per year.

**Fig. 2. Seasonal correlations of annual black spruce growth (1960–2004) with temperature, precipitation, and SMI.** Seasons include prior-year spring (May and June), summer (July and August), fall (September and October), and winter (November to April) and the current-year spring and summer. Black contours around each circle indicate significant correlations ( $P < 0.05$ ) from 1000 bootstrap replicates. Of the 378 tree-ring width chronologies, 290 (77%) display at least one significant correlation with one of the three seasonal climate variables. The 49th parallel north is indicated by a dotted line. Because the soil-drying model used to estimate the SMI is designed and calibrated for the snow-free season, we did not calculate the correlation of winter SMI with growth.



**Fig. 3. Latitudinal and temporal shift in temperature, water availability, and growth response.** (A) Average MAT and MAP of study forests (1960–2004) binned by 0.1° latitude. Data are means  $\pm$  SEM. Temperature decreases linearly with latitude ( $P < 0.001$ , two-tailed  $t$  test), unlike precipitation ( $P > 0.05$ ). (B) Proportion of positive correlations with growth ( $P < 0.05$ , stationary bootstrap) across seasons, binned by degree of latitude. Asterisks indicate values differing significantly from 0.5 ( $P < 0.05$ , two-tailed chi-squared tests). Linear regression model  $P$  values for slopes of temperature, precipitation, and SMI are  $< 0.01$ ,  $0.11$ , and  $< 0.01$ , respectively (one-way analysis of variance models). Forests above 49°N display significant patterns of low-temperature constraint. (C) Areas with baseline (1971–2000) and future (2041–2070) MAT corresponding to the forests with low-temperature constraints from (B). Colors indicate the 10th, 50th, and 90th percentiles of projected MAT from 21 climate simulations and two greenhouse gas emission scenarios [representative concentration pathways (RCPs)] of 4.5 and 8.5  $W m^{-2}$  (35).



correlations with SMI are positive between 47° and 49°N and become negative above 50°N. As for precipitation, the majority of the significant correlations are negative above 51° to 52°N (Fig. 3B). To summarize, all three climate variables point toward a low-temperature constraint in black spruce forests north of approximately 49°N. The average MAT of forests sampled at this latitude is  $1.1 \pm 0.7^\circ\text{C}$  (SD) and may be a threshold of MAT below which the growth of black spruce trees is constrained by low temperatures (Fig. 3C). In contrast to typical climate envelope models, which use species distribution data to estimate their climatic niche, our approach uses the climate sensitivity of thousands of black spruce trees.

According to median temperature projections for a low- and a high-emission scenario (4.5 and  $8.5 \text{ W m}^{-2}$ ) for 2041–2070, 63 to 80% of the territory from 49° to 52°N should still be subject to MAT associated with positive temperature responses (Fig. 3C). Considering that (i) increasing growth rates are being reported at the species treeline [55° to 58°N (18)] and (ii) the species is already dominant at these latitudes although at lower density, we see no major constraint against a shift of the refugium into the open-crown forests located north of the study area, despite the presence of less fertile soils. We acknowledge that there is a potential warming threshold when the region would lose its capacity to favor black spruce growth.

The essentially monotypic black spruce boreal forest dominating at latitudes from 49° to 52°N has a largely positive growth response to the combined increase in temperature and decrease in precipitation, thus supporting the hypothesis that low temperatures are the dominant climatic growth constraint. Conversely, growth reductions associated with increases in temperature and decreases in precipitation and SMI are mostly found south of 49°N. This conclusion agrees well with (i) satellite-derived observations of recent increases in photosynthetic activity in high-latitude forests of NENA (12, 13, 33), (ii) ground-based reports of a recent increase in black spruce growth in the northern forest-tundra of NENA (18), and (iii) predictive growth models for boreal tree species of NENA (17). The poor adaptation of black spruce to warm temperatures (6) that is responsible for its lower relative abundance south of 49°N (fig. S1), coupled with the higher water requirements of the denser, taller, and more productive forest stands found at these latitudes, may contribute to the observed response gradient. Being mainly driven by temperature, this gradient is likely to also affect other boreal species of NENA, although species-specific adaptations at the scale of this study are unknown.

In contrast to the moisture-sensitive boreal forests of central and western North America, results from this heavily replicated network indicate that eastern black spruce populations north of 49°N show no sign of a negative response to climate warming and instead respond positively to increased temperature and reduced precipitation. Although these conclusions do not take into account the predicted changes in biotic and abiotic disturbances (2), they do suggest that the higher

NENA water availability could allow boreal tree species such as black spruce to better withstand a warmer climate in NENA than in the central and western portions of North America. Outside of the potential for extreme disturbance events, NENA may act as a refugium for the boreal forest.

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#### SUPPLEMENTARY MATERIALS

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#### ECOSYSTEM SERVICES

## Improvements in ecosystem services from investments in natural capital

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In response to ecosystem degradation from rapid economic development, China began investing heavily in protecting and restoring natural capital starting in 2000. We report on China's first national ecosystem assessment (2000–2010), designed to quantify and help manage change in ecosystem services, including food production, carbon sequestration, soil retention, sandstorm prevention, water retention, flood mitigation, and provision of habitat for biodiversity. Overall, ecosystem services improved from 2000 to 2010, apart from habitat provision. China's national conservation policies contributed significantly to the increases in those ecosystem services.

**T**hrough pursuit of rapid economic development, China has become the second largest economy in the world and has lifted hundreds of millions of people out of poverty since the “reform and opening up,” begun

in the 1970s. Yet the costs of this success are reflected in high levels of environmental degradation. In 1998, massive deforestation and erosion contributed to severe flooding along the Yangtze River, killing thousands of people, rendering 13.2 million



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Editor's Summary

**A future for boreal forests**

Conservation under climate change presents the challenge of predicting where will be suitable for particular organisms and ecological communities in the future. D'Orangeville *et al.* assess the probable future range for boreal forests in eastern North America, which are expected to be subject to large temperature increases in their natural range. Using tree-ring data from many thousands of forest stands, they delineate the geographical extent of the region where tree growth responds favorably to higher temperatures and where the forest should persist at least until 2070.

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