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RESEARCH ARTICLE

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Surprisingly wide climatic niche breadth of a relict mountain species raises hope for survival under climate change

Yaacoub Nassif[1] | Paulina E. Pinto[1,2] | Juan Fernandez-Manjarres[3] | Jean-Claude Gegout[1,2]

[1]Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France

[2]Harvard Forest, Harvard University, Petersham, Massachusetts, USA

[3]Univ. Paris Sud, CNRS, Lab Ecol, Systemat Evolut, Orsay, France

Correspondence
Paulina E. Pinto, Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France.
Email: paulina.pinto@agroparistech.fr

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Abstract

Aims: We assessed the juvenile climatic niche breadth of a relict mountain species by comparing field observations and transplant experiments within and beyond the elevational limits of its distribution range.

Location: Lebanon – Near East – Mediterranean region.

Methods: We studied the survival and growth of the Cedar of Lebanon (*Cedrus libani*) to determine the lower and upper elevational range limits of its juvenile stage through an experimental setup with and without water supplementation and with potentially competing species as a control. The experiment included eight common gardens at elevations ranging from 110 to 2330 m, within and far beyond the warm and cold limits of Cedar distribution observed under natural conditions.

Results: We observed unexpectedly high survival and growth rates of Cedar at elevations well below the range of its natural distribution in Lebanon. Below the observed warm limit, water stress at very low elevations and competition at low and medium elevations limited juvenile survival. In contrast, cold temperature and water stress limited survival at elevations slightly above the observed upper natural limit. The experimental setup demonstrated that the elevation range suitable for Cedar growth and survival was twice as wide as the range within which Cedar is observed under natural conditions.

Main Conclusions: High survival rates experimentally observed beyond the warm limit of the natural distribution range of the Cedar of Lebanon raise hope for its resilience to ongoing climate warming. If this pattern were frequent among montane species, it would challenge predictions of massive extinction with climate change and pave the way for promoting adaptive actions such as competition management to improve their survival.

KEYWORDS
Cedar of Lebanon, climate change, common garden, lower elevational range limit, Mediterranean region, range limits, realized niche breadth, upper elevational range limit

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1 | INTRODUCTION

Understanding the range-limiting drivers of species is essential for predicting the distributional changes expected to result from climate change (Doak & Morris, 2010; Parmesan et al., 2005; Rumpf et al., 2019; Xiao et al., 2022). Despite sustained theoretical interest (Godsoe et al., 2017; MacArthur, 1972) and a flurry of research on species distribution over the past decades, the ecological constraints that drive short-term range limits remain poorly understood (Gaston, 2009; Lyu & Alexander, 2022; Sexton et al., 2009). The cold range limits of plant species appear to be caused by restrictions on plant growth or reproduction as a result of cold temperature (MacArthur, 1972; Morin et al., 2007; von Büren & Hiltbrunner, 2022). However, observations carried out in the Mediterranean zone also highlight the role of the summer period on oak species upper elevational limit (Bar-on et al., 2022). Likewise, ecophysiological approaches have showed an important role of hydric conditions combined with temperature on the survival of seedlings at the cold limit of the distribution range of a Pine species (Moyes et al., 2015).

On the other hand, biotic interactions are often considered to be the main drivers of the occurrence of many species within their warm limits (Brown et al., 1996; MacArthur, 1972; Pellissier et al., 2013) or at the niche scale (Schellenberger Costa et al., 2018). At the scale of tree species distribution, several authors have suggested that climate – especially water availability – may be involved in the localization of the warm limit, in addition to biotic factors (Cahill et al., 2014; Castro et al., 2005; Hampe & Petit, 2005).

Climate projections show a rapid continuation of warming for the coming century. This makes it unlikely that the current correlation between species distribution and the climate they evolved in will be maintained (Richard et al., 2021). This mismatch is expected to entail poor adaptation of trees to their new environments and a possible loss of forest productivity (Aitken et al., 2008). It also raises the question of how to better understand the ultimate causes of species distribution limits. The challenge is twofold: (i) to determine whether it is now possible to implement assisted migration of species beyond their current cold limit to sites that will be climatically favourable to them at the end of the century; and (ii) to assess whether future conditions across their current distribution range, which will probably be warmer and drier than presently, will still be favourable to their survival.

Given the risks of desertification in the Mediterranean region and the paucity of studies, it is essential to increase our knowledge about the climatic limits of Mediterranean species in order to better assess their vulnerability to climate change. Observations and simulations show that climate change in the Mediterranean area is going to be more intense and rapid than in the temperate zone (IPCC, 2021). The bulk of the experimental work done to date to test species distribution limits has primarily focused on temperate species and their cold limits, making it possible to explore the expansion of their ranges within certain limits (Hargreaves et al., 2014). In contrast, results about the very few Mediterranean species studied to date suggest that warming is likely to lead to forest regression in favour of desert vegetation, particularly in the eastern Mediterranean regions (Guiot & Cramer, 2016; Jimenez-Alfaro et al., 2016; Vennetier & Ripert, 2010).

Among the Mediterranean tree forest species, the Cedar of Lebanon (*Cedrus libani* A. Rich.) is a structuring species of the Middle Eastern montane forests, located in the south of its distribution range (Talhouk et al., 2001), at the margin of desert formations. Its presence mainly in the montane zone makes it particularly vulnerable to the strong impact of current climate change on Mediterranean mountains (Regato & Salman, 2008). Simulations of its future geographical distribution in Lebanon based on its current distribution have been carried out for the 2070–2100 period. They predict the near disappearance of this species, with only three areas in Mount Lebanon where it could survive (Hajar et al., 2010). More recently, Xiao et al. (2022) also predicted the potential disappearance of stands of *C. libani* in high-elevation habitats with future climate warming by the end of the century.

In Lebanon today, Cedar populations barely cover 2200 ha and are located mainly on the western slopes of Mount Lebanon, at elevations between 1100 and 1950 m (Khuri et al., 2000). There are also a few thousand widely scattered trees above 1000 m in Syria and above all more than 300,000 ha in the Taurus Mountains in Turkey, generally between elevations of 1500 and 2000 m (Boydak, 2003; Quezel, 1998). Ecological knowledge of the temperature and precipitation ranges that limit the distribution of the Cedar of Lebanon is limited. Distribution models based on occurrence data from the Global Biodiversity Information Facility (GBIF) database show a key role of winter precipitation and temperature on the natural distribution of *Cedrus* species. These models also highlight the importance of summer precipitation on the distribution of *Cedrus* spp. in the Mediterranean region (Xiao et al., 2022). However, ecological and ecophysiological information available for the Cedar of Lebanon is still insufficient to precisely specify the key factors of the limits of its natural distribution range.

We sought to determine whether the limits of the natural elevational range of the Cedar of Lebanon coincided with the limits of its climatic niche breadth. We followed the definition of a niche of Schellenberger Costa et al. (2018, and references therein) as 'a multidimensional volume in environmental space in which species maintain self-sustaining populations in the presence of biotic interactions' and niche breadth as 'the occurrence range of a species along an environmental gradient'. Our approach included comparing key fitness parameters of the species within and outside its natural elevational range and investigating the ecological causes of its disappearance outside its limits. We sought to answer the following four questions:

1. What are the lower and upper elevational range limits of the Cedar of Lebanon observed under natural conditions?
2. How do survival and growth at the seedling stage shape the upper and lower elevational range limits of Cedar?

3. What is the role of temperature and water stress in determining the limits of the elevational range of Cedar?
4. What evidence of potential inter-species competition at the juvenile stage can be deduced from control tree species planted under the same conditions as Cedars?

To answer these questions, we conducted a common garden transplanting experiment consisting of eight experimental sites evenly distributed along an elevational gradient ranging from 110 to 2330 m in northern Lebanon. Two treatments – watered/non-watered – were performed at each site to examine the effects of thermal and water constraints on the elevational range limits of Cedar. To estimate the potential role of competition, the growth and survival rates of Cedar were compared with those of the three most competitive tree species in the region, which were planted and measured simultaneously on the experimental sites using the same experimental design as that of Cedar.

2 | METHODS

We used two complementary approaches to achieve the expected objectives: (a) observations in natural Cedar forests and (b) an experimental setup including eight common gardens at elevations ranging from 110 to 2330 m. In order to accurately determine the elevational range of the Cedar of Lebanon under natural conditions in northern Lebanon, we recorded the presence/absence of Cedar in 1023 sites located outside urban areas and plantations. The design included 750 field vegetation surveys and 273 sites with a low tree-cover and located at high elevation, that were visually checked for the presence/absence of *C. libani* using satellite imagery (Figure S1a). The sites harbouring Cedar were used to define the elevational range of the species in northern Lebanon. The warm and cold limits of Cedar distribution under natural conditions were defined by the 5th and 95th quantiles of the elevational distribution of Cedar occurrences (Stahl et al., 2014).

Cedar occurrences across its geographical range in Lebanon, Turkey, Syria and Cyprus were also extracted from the GBIF database to provide a comprehensive estimate of the climatic niche of the species and to verify that the experimental design extended beyond the cold and warm limits of its temperature range. Out of 265 selected sites with geographical coordinates, 89 were kept (Figure S1b) and 176 were excluded after photointerpretation of each site on Google Earth because they did not include Cedar in natural conditions, or were located in cities, farmlands, Cedar plantations, or landscape parks or were spatially redundant with the selected sites (present within 0.001° latitude and longitude of a selected site).

In parallel to Cedar observations in natural conditions, an experiment was set up in northern Lebanon along Kadisha Valley (Figure 1a). This region is at the heart of the distribution range of Lebanese Cedar populations, so that an elevational gradient ranging from 0 to 3000 m can be covered within a few tens of kilometres. Given that the elevational range of Cedar provided by the literature extends between elevations of approximately 1100 and 1950 m (Khuri et al., 2000), eight experimental sites were established at regular intervals between 110 and 2330 m in order to include the medium, cold and warm limits of the distribution range and far beyond (Figure 1a). Table 1 shows the key climatic parameters of each experimental site.

Sites with optimal soil conditions have been selected to highlight the effects of climate in the absence of edaphic constraints. Since the Cedar of Lebanon grows essentially on calcareous or calcaro-dolomitic substrates (Boydak, 2003; Quezel & Barbero, 1985), the experimental sites were set up in a calcareous environment (except

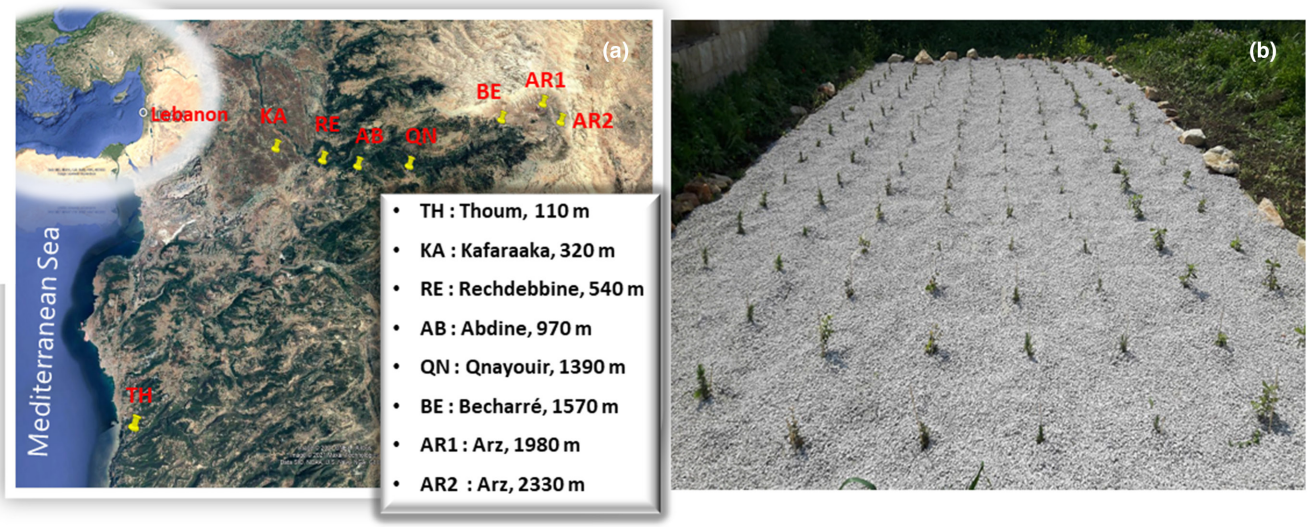


FIGURE 1 Distribution of the eight common gardens of the experimental setup between 110 and 2330 m elevation, mainly along Kadisha Valley in northern Lebanon (a) and photograph of the non-watered batch in Thoum site in 2019 (b). Top left inset, position of the study area in the Middle East. *Source*: Google Earth.

TABLE 1 Localization, elevation and mean climate conditions of the eight experimental sites installed in northern Lebanon along Kadisha Valley over the 1980–2010 period.

Site	LON	LAT	ELV	MAT	M1T	Min1T	MAP	M456P	M789P
1	35.657	34.211	110	19.7	13.3	11.1	1321	98	12
2	35.839	34.319	320	18.4	11.0	7.9	1391	113	13
3	35.867	34.294	540	17.6	9.7	6.2	1276	108	12
4	35.889	34.277	970	15.0	6.7	3.0	1333	115	13
5	35.926	34.258	1390	12.6	3.8	−0.2	1357	122	15
6	36.019	34.253	1570	10.5	1.1	−3.2	1082	105	13
7	36.061	34.247	1980	8.1	−1.5	−6.0	1059	106	14
8	36.061	34.227	2330	5.8	−3.9	−8.3	1035	104	14

Abbreviations: ELV, elevation (m a.s.l.); LAT, latitude (decimal degrees); LON, longitude (decimal degrees); M1T, mean temperature in January (°C); M456P, mean total precipitation in April, May and June (mm); M789P, mean total precipitation in July, August and September (mm); MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C); Min1T, mean minimum temperature in January (°C).

Source: CHELSA v2.

for the site located at 970 m elevation) on deep (>40 cm) ploughed soils, cleared of large stones and with a predominantly clayey texture. The effects of exposure and slope were minimized by installing the sites in topographic situations with a slope of less than 3% (except the two sites located at high elevations). As the Cedar of Lebanon is heliophilic (Boydak, 2003), the sites were installed in full light. They were also covered with canvas and gravel and regularly weeded manually to avoid any competition from herbaceous species (Figure 1b). Finally, all the sites were protected from grazing by an enclosure, except the two high-elevation sites located in ungrazed, supervised areas.

Cedar seeds were collected in April–May 2018 from three natural stands at the lower (1232 m) and upper (2011 m) limits of its elevational range in northern Lebanon and at 1431 m in the centre of its elevational range. Seeds of the three competitors of Cedar under natural conditions – *Pinus brutia* Ten., *Quercus calliprinos* Webb. and *Quercus infectoria* Oliv. – were also collected at the low, medium and high limits of each species' elevational range in natural forests in northern Lebanon, at the same period for pine and in November–December 2017 for the two oak species. Cedar seeds and seeds of the other species were planted in pots immediately after harvesting. All seedlings were transplanted to the experimental sites in fall 2018. Seedlings from low, medium and high elevation were distributed evenly between the sites and treatments, at each site and for each tree species.

Seedlings were planted in the batches at a constant 50-cm spacing to allow them to grow freely during their juvenile stage. A total of 576 Cedars were planted (72 per site). The seedlings of the three competitive species – *Q. calliprinos*, *Q. infectoria* and *P. brutia* – were planted on the same sites and exactly in the same conditions as those selected for Cedar.

At each site, half of the individuals of each species were exposed to watering (as a control) and the other half to non-watered conditions (representing natural conditions) to study seedling survival and growth in the absence/presence of the summer water stress. Finally, 36 individuals of each species including 12 individuals from low elevation, 12 from medium elevation and 12 from high elevation were planted in each watered/non watered batch in each site. To ensure recovery after transplanting, both the watered and non-watered batches were watered in 2019 during the first growing season after transplanting. Watering was discontinued for the non-watered batch after the first rains in the fall of 2019. To water the plants, 2000-litre water tanks were installed on the sites located between 110 and 1980 m above sea level. Water was supplied by a pipe system allowing drip irrigation of each plant. Watering was done by emptying the tanks by gravity every 2 weeks, so that each plant of each 'watered' batch was supplied with approx. 13.9 L of water twice a month. At the site located at an elevation of 2330 m, we watered the plants manually using a garden hose connected to a water retention basin located at 2450 m elevation. The start of the watering season varied according to elevation: watering was carried out from April 15 at the sites between 110 and 1570 m above sea level and started from June 15 at the sites located at 1980 and 2330 m above the sea level. Watering ended each year with the first fall rains.

The experiment lasted 3 years – from fall 2018 (planting) to fall 2021 (last measurements). Tree height, diameter at the base of the stem and survival were measured in October of each year, after the growing season. These measurements were used to calculate survival rates and average growth in diameter and height for each site, species and watering treatment.

Survival rates of Cedar were first graphically analysed along the elevation gradient for the watering and non-watering treatment. A logistic regression model was then calibrated between the binary variable alive/death, corresponding to observed survival after 3 years, as the dependent variable and elevation, watering/non-watering variables as predictors. The statistical significance of the predictors was set up at $\alpha = 0.05$. Growth differences after 3 years between watered and non-watered treatments were analysed by performing a *t*-test for each experimental site. The level of statistical significance was set at $\alpha = 0.05$.

Measuring all dimensions of competition was not feasible, so we focused on early growth indicators as proxies of inter-species

competition. Height growth is a well-known strong indicator of competitiveness (Gaudet & Keddy, 1988; Tanner et al., 2005; Westoby et al., 2002). During forest stand development, access to light is a key determinant of tree competitiveness, which is directly linked to the growth capacity. The competitiveness of Cedar along the elevational gradient was analysed by comparing its radial and height growth in each site with those of its competitor species planted at the same elevation and in the same conditions. A one-way analysis of variance (ANOVA) test ($\alpha = 0.05$) was performed to examine the statistical significance of growth differences observed between Cedar and its competitors species. All figures and analyses were conducted using R v.4.2.1 (R Core Team, 2022).

To characterize the climatic distribution of the Cedar of Lebanon and position our experimental setup, we extracted temperature and precipitation data from the CHELSA v2.1 database (Karger et al., 2017, 2021) for each of the 1023 vegetation surveys recorded with the presence/absence of Cedar, the 89 GBIF vegetation surveys and the eight experimental sites.

3 | RESULTS

3.1 | Elevation and climatic ranges of Cedar

The analysis of the presence/absence of Cedar in the 1023 vegetation plots surveyed under natural conditions in northern Lebanon showed that Cedar populations can be spotted from 1300 m elevation (5th percentile of occurrence) and are mainly located between 1340 and 1710 m (25th–75th percentiles), with an elevational optimum at 1540 m. They strongly regress at around 1830 m elevation (95th percentile of occurrence), where they constitute the forest limit of the closed canopy stands of the region. In the forests of northern Lebanon, the mean annual temperatures corresponding to the 5th and 95th percentiles of the elevational range of Cedar are 12.3 and 9.1°C, respectively (Figure 2a, CHELSA v2, annual mean temperatures for the 1980–2010 period). Under natural conditions, the Cedar appears to grow within a narrow thermal range of a few degrees around an annual mean of 11°C. It can survive harsh climatic conditions: the average minimum temperature of the coldest month reaches 0°C in Lebanon (Figure S2a) and even drops to −4.4°C at the scale of the species range (Figure S2b). The mean annual precipitation is around 1300 mm across its elevational range in northern Lebanon (Figure 2a), but it can be present under lower annual rainfall in other parts of its geographical range (Figure 2b). Limiting water conditions occur in the summer period in Lebanon, when precipitation is very low (around 15 mm from July to September), whereas it can reach 80 mm in other parts of its geographical range (Figures S2a,b). Finally, the temperature and precipitation range is wider throughout the geographical range of Cedar than in Lebanon, which represents the southern limit of its range (Figure 2a,b).

3.2 | Cedar survival and height growth along the elevational gradient

Under natural water stress conditions corresponding to the 'non-watered' treatment, the survival rates of Cedar decreased over time only at the two extremes of its elevational gradient: low survival

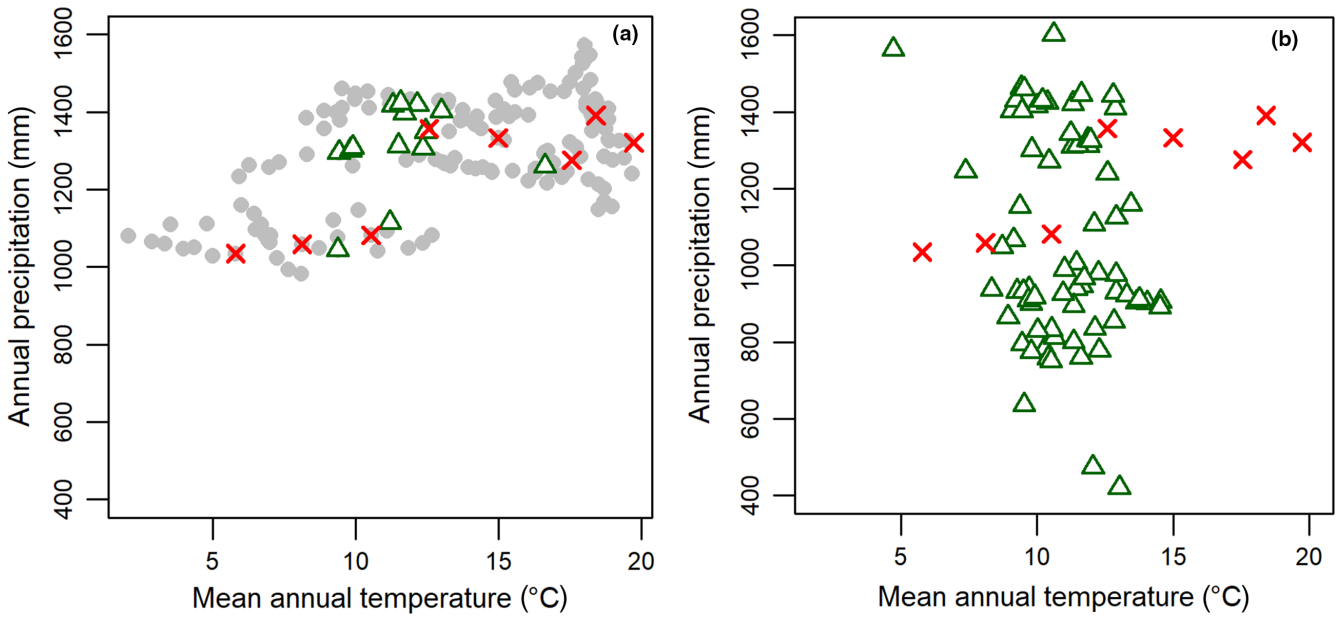


FIGURE 2 Distribution of Cedar of Lebanon vegetation surveys across the study area in northern Lebanon (a) and across its entire geographical range (b, *Source*: GBIF) according to mean annual temperature and mean annual precipitation. The climate characteristics of the eight experimental sites are added in panels (a) and (b). Green triangles, vegetation surveys where Cedars were present; grey dots, vegetation surveys where Cedars were absent; red crosses, experimental sites. Climate values were averaged for the 1981–2010 period (*Source*: CHELSA v2).

rates (25%–60%) occurred after 3 years for the seedlings growing below 500 m elevation. High survival rates close to 100% were observed for the seedlings growing between 500 and 1700 m elevation. The survival rates of the non-watered seedlings gradually decreased to 72% above 1900 m elevation (Figure 3a).

The height of Cedar seedlings in non-watered conditions varied between 16 and 62 cm on average depending on elevation at the end of the experiment (Figure 3b). Except for the only site located at 970 m on non-carbonate substrate, the mean height of Cedars was greater than 40 cm from 100 to 1700 m elevation. In contrast, it decreased at elevations above 1700 m, down to 16 cm at 2330 m elevation.

3.3 | Effects of water stress and temperature on the Cedar survival and height growth along the elevational gradient

The survival rate of *C. libani* in the 'watered' treatment, i.e., in the absence of water stress, was above 86% along the elevational gradient (Figure 3a). It was higher than 97% between 540 and 1570 m elevation and slightly lower at the most extreme sites at the highest and lowest elevations. The constant and high survival rate of the 'watered' Cedars along the elevational gradient compared to the lower survival rate of the 'non-watered' Cedars at climatic extremes highlights that the survival rate of *C. libani* seedlings is more sensitive to water stress than to temperature both at its lower and upper elevation range limits (Figure 3a). The logistic regression performed between Cedar survivals and elevation and water treatment as predictors showed that elevation, water stress and their interaction on the survival of Cedar were all highly significant ($p < .0001$). Water stress at the lower elevation extreme appeared to have a stronger effect compared to its effect at higher elevations (Figure S3).

The statistical *t*-test revealed that the average height of the 'watered' Cedars after 3 years was not significantly greater than that of the 'non-watered' Cedars (Figure 3b), except at the site located on a non-carbonate substrate at 970 m elevation. This suggests that watering only improves the survival rate of Cedars at lower and higher elevations, without any significant effect on growth rates.

3.4 | Effect of interspecific competition on Cedar along the elevational gradient

At very low elevations (below 500 m), the survival rates of the 'non-watered' Cedars were lower than those of the other Mediterranean forest species studied in the experiment (Figure 4a). Between 500 and 1500 m elevation, the survival rates of *C. libani* and its potential competitors were almost 100%. At very high elevations (from 1900 m), *C. libani* was the only species that withstood the climatic conditions of these mountainous areas: *P. brutia*, *Q. calliprinos* and *Q. infectoria* individuals had almost all died 3 years after planting.

Cedars exhibited the lowest growth in stem height and diameter at 110 m elevation under natural conditions (non-watered treatment) compared with *P. brutia* (one-way ANOVA, $p < .001$ for height and $p < .001$ for diameter), *Q. calliprinos* ($p < .001$ for height and $p < .01$ for diameter) and *Q. infectoria* ($p < .001$ for height, $p < .05$ for diameter) (Figure 4b,c). Their low relative growth remained unchanged under watered conditions (Figure S4). They also grew less than *Q. infectoria* and particularly *P. brutia* below 900 m elevation ($p < .0001$ for height and diameter), both under non-watered and watered conditions (Figure 4b,c, Figure S4). The average height and diameter of the three-competitor species were respectively 57.1% and 18.6% greater than those of Cedar below this elevation threshold in non-watered conditions. On the other hand, Cedar displayed similar or higher growth rates than its three potential competitors at elevations above 900 m. Its mean height and diameter were 6.0% and 7.8% greater than those of the other species in non-watered conditions (Figure 4b,c).

4 | DISCUSSION

4.1 | Is the upper elevational range limit of Cedar limited by cold temperature or water stress under natural conditions?

Beyond the upper elevational limit of Cedar seedlings observed under natural conditions, their survival rate progressively decreased in parallel with a sharp decline in growth. This drop in the fitness of Cedar beyond its cold limit is consistent with most results found for other species in transplant experiments (Hargreaves et al., 2014; Lee-Yaw et al., 2016). The important effect of water supply highlighted by the experiment was not anticipated to such an extent since the cold margin of a species range is typically associated with thermal constraints (Brown et al., 1996; Körner et al., 2016), sometimes biotic interactions (Armitage & Jones, 2020; Carter & Prince, 1985) or historical limits of dispersion (Svenning et al., 2008). However, our findings are consistent with drought constraints on Mediterranean treelines (Körner, 2012) and the strong impact of water stress on seedling establishment at the treeline in the Rocky Mountains (Lazarus et al., 2018; Moyes et al., 2015). As showed by Bar-on et al. (2022), winter conditions end later at higher elevations, while summer drought begins at around the same time across the elevation gradient in Mediterranean areas. This double constraint leads to a reduction of the length of the growing season as elevation increases. By relieving the summer drought stress, watering in our experiment extended the growing season and promoted the high survival rate of juveniles at the highest elevations.

4.2 | Lower elevational range limit of Cedar: water stress, competition or history?

Our study suggests that below the warm elevational range limit of the Cedar of Lebanon under natural conditions, the survival rate of its seedlings was high down to 500 m elevation and then progressively

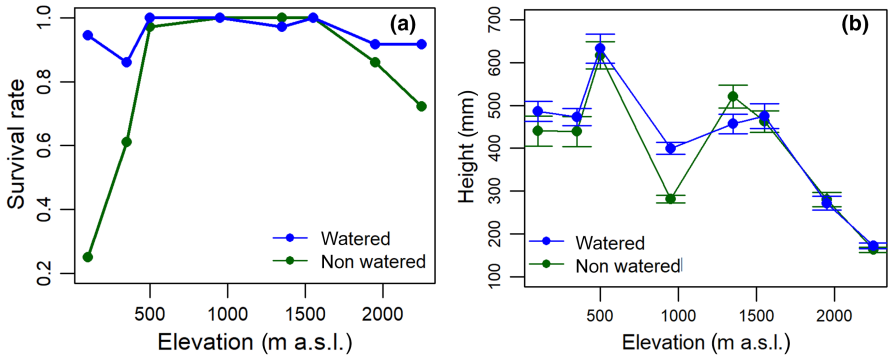


FIGURE 3 Effect of watering on the survival rate (a) and growth rate (b) of 3-year-old Cedars of Lebanon along a 110–2330 m elevation gradient in Lebanon. Error bars, SEs.

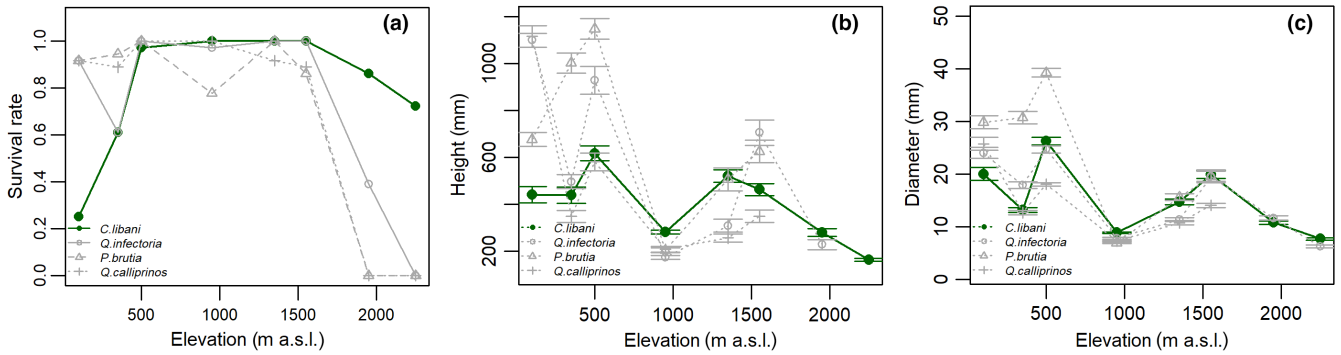


FIGURE 4 Effect of interspecific competition on Cedars of Lebanon along an elevational gradient in non-watered conditions: (a) elevational change of the survival rates of Cedar and its competitors (*Pinus brutia*, *Quercus calliprinos* and *Quercus infectoria*); (b) development of the stem height of Cedar and its three competing species along the elevational gradient (mean height of all surviving individuals of each species); (c) development of the stem diameter of Cedar and its three competing species. Error bars, SEs.

decreased towards low elevations. This 500-m elevation limit at which Cedar survival is still optimal is much lower than the present range limit of 1300 m elevation observed under natural conditions. The absence of Cedar below its currently observed lower margin under natural conditions might be explained by a cumulative effect of three factors, namely water stress, competition and history.

4.2.1 | Water stress as a limiting factor at very low elevations (<500 m)

Below 500 m elevation, the different survival rates of the watered and non-watered Cedars suggest that summer water stress – characteristic of Mediterranean climates – was directly linked with the high mortality rate of the seedlings. The effect of high temperature appears to be very small at this low elevation, as survival rates were high when summer water shortage was offset by watering. Our results are consistent with recent species distribution models that show the importance of summer precipitation for the survival of Cedar species in the Mediterranean region (Xiao et al., 2022). They also agree with those of Castro et al. (2005) who showed that summer drought was responsible for 50%–75% of the mortality of Scots pine (a boreal tree species) seedlings at the southernmost limit of its distribution range in the Mediterranean area and that drought was still causing high mortality up to 4 years after emergence.

4.2.2 | Inter-specific competition as a limiting factor at low/middle elevations (500–900 m)

Several biotic interactions can act to constrain the presence of Cedar including grazing, which is important in rural areas of Mediterranean landscapes (Perevolotsky & Haimov, 1992), and competition. The change in intensity of these interactions with elevation may explain the limit of Cedar between 500 and 900 m. In our experiment, we focused on competitiveness between Cedar and its main competitor species. Measurements were made under free-growing conditions in pure stands. Relative height growth differences between species highlighted along the elevational gradient may be relevant proxies for growth performances under natural conditions in pure stands at the regeneration stage, as height growth is not very sensitive to stem density in pure stands (Skovsgaard & Vanclay, 2008). In mixed stands, differences in height growth between species may change with stand age or depending on the species in the stand (del Río et al., 2016). In this case, our experiment can only provide a preliminary assessment of species competitiveness. However, at elevations between 500 and 900 m, the competitors of Cedar seemed to have an important competitive advantage: the growth of *Pinus* and *Quercus* species was approximately twice that of Cedar for the fastest growing species (which varied among experimental sites). Cedar's low growth rate in height and diameter compared to that of its three potential competitors could be a major cause for its absence in this elevational belt.

This hypothesis is well supported by the fact that *P. brutia*, *Q. calliprinos* and *Q. infectoria* have their ecological optimum within this elevational range (Abi-Saleh et al., 1976). The limitation of the lower latitudinal or elevational range limit by interspecific competition has long been suggested (Darwin, 1859; MacArthur, 1972). It has been studied in natural conditions (Leathwick, 2002; Vetaas, 2002) and supported more recently by transplant tests and field experiments (Hargreaves et al., 2014; Paquette & Hargreaves, 2021). However, the respective importances of biotic and abiotic effects on distribution limits at the scale of the species range remain difficult to establish (Godsoe et al., 2017; Louthan et al., 2015). By showing that competition can act over an elevational range of several hundred metres within the favourable range of Cedar survival, the experimental setup used in our study provides new insights on the importance of biotic factors in shaping species distribution limits.

4.2.3 | Historical human impact as a limiting factor of Cedar distribution at mid-elevations (900–1300 m)

There is ample historical evidence of the use of this noble, rot-proof wood with a large volume *per* stem at maturity by great civilizations – Egyptians, Babylonians, among others – that succeeded one another in the Middle East. Lebanese Cedar forests have been strongly impacted by urbanization, grazing and especially timber cutting from the Neolithic period until the last century (Hajar et al., 2010; Loffet, 2004). Consequently, large removals of Cedar as a result of increased human activities since before 2000 BP could explain its current absence in favourable climatic and competitive conditions. For example, Cedar has been used for shipbuilding, construction and Egyptian sarcophagi (Hepper, 2001). The scribe of Pharaoh Snefru mentions the arrival of 40 ships loaded with Cedar wood in Egypt around 2600 BP (Liphshitz & Biger, 1991). Finally, Byblos, located near the main Cedar forests in north Lebanon, was the main port used to export Cedar timber during Antiquity (Hepper, 2001; Liphshitz & Biger, 1991). This could explain why the main stands that were removed were those closest to the sea at low elevation. The possible human-induced near-extinction of Cedar between 900 and 1300 m in Lebanon is also partly supported by its historical presence at 900 m elevation in the Bekaa Plain around 2000 BP (Hajar et al., 2010) and by its current presence between 1000 and 1300 m in Turkey, which suggests that Cedars could exist at these elevations under natural conditions.

4.3 | Discrepancy between the narrow elevation range of Cedar and its large temperature niche breadth

Under current climatic conditions in Lebanon, our experimental setup suggested for the first time that the Cedar of Lebanon could grow within a climatically favourable elevation range of 1500 m, which is almost three times the currently observed range. This wide range of suitable elevations reveals that juvenile Cedars can survive within a much larger mean annual temperature range than that expected based on the elevation range within which Cedar forests are currently found in Lebanon. The dispersal of Cedar beyond its upper elevational range limit could be prevented in natural conditions by climatic parameters (cold temperature and water stress) characteristic of high elevations of Mediterranean mountains. Below its warm elevational limit, the combination of three factors could explain the absence of Cedar: water stress at very low elevations (<500 m), biotic interactions (competition) at low/middle elevations (500–900 m) and human history at medium elevations (900–1300 m). Our results agree with those of Cahill et al. (2014) and Paquette and Hargreaves (2021), who alternately put forward climate variables or biotic interactions depending on the species to explain the warm limit of the species. The large elevation range covered by our experimental design highlights the importance of both abiotic and biotic factors in setting the elevational limit of the Cedar range. It allowed to distinguish between the part of the elevational gradient unsuitable for Cedar due to water stress constraints and the part likely unsuitable due to competition constraints. Furthermore, the experimental setup showed that a high tree growth rate can occur below the lower elevational limit. High growth and survival rates of sugar maple have been observed near and beyond the southern limit of its distribution range (Putnam & Reich, 2017). Larger biomass and height of species have also been observed when individuals were transplanted within the species elevation range at a lower elevation than their site of origin (Midolo & Wellstein, 2020). The high rates of survival and growth of the Cedars of Lebanon transplanted below their currently observed warm limit complement the results of these authors by highlighting the potential for species to exhibit high performance beyond the warm limit of their geographical range in the absence of biotic limitation.

4.4 | Long-term conservation and the management of Cedar

Our field observations are in stark contrast with our experimental set-up, and confirm the relictual character of the Cedar forests currently present in Lebanon. They also suggest that the survival of current stands may not be directly threatened by ongoing global warming and the related temperature or water stress changes because Cedar seedlings survived in warmer conditions than those occurring in the Cedar forests of Lebanon today. These relictual populations could be increased according to a two-fold strategy. Firstly, the very low mortality rate of Cedar in watered conditions at very high elevation suggests that it seems possible to use assisted migration beyond the cold limit of natural stands if water is added in the first years after planting. However, the low growth rate at high elevation would imply leading this operation for landscape or ecological restoration purposes rather than wood production. Secondly, the Cedar of Lebanon could probably

be introduced at an elevation lower than its natural low limit throughout the supra-Mediterranean belt whose elevational limits in Lebanon range between about 1000 and 1500 m (Abi-Saleh et al., 1976). However, ongoing global warming will increase the relative competitiveness of its competitors at the lowest elevations. This might require more management operations aimed at eliminating broad-leaved species that could prevent Cedar growth through competition.

5 | CONCLUSIONS

The present research work renews the interest in studying the juvenile climatic niche breadth of relict mountain species considered highly threatened by climate change at the global scale. If the pattern observed for the Cedar of Lebanon is generalizable to other tree species, it would highlight lower-than-expected vulnerability of these species, as well as avenues for conservation and adaptation via planting and competition management.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this manuscript will be made freely available on Dryad upon publication of the manuscript. Dryad. https://doi.org/10.5061/dryad.k0p2ngfdf.

ORCID

Paulina E. Pinto https://orcid.org/0000-0002-1628-1826
Juan Fernandez-Manjarres https://orcid.org/0000-0002-2479-9289
Jean-Claude Gegout https://orcid.org/0000-0002-5760-9920

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BIOSKETCHES

Yaacoub Nassif is a PhD candidate at AgroParisTech. He investigates the climatic drivers of realized climatic niches of Mediterranean plant species. **Paulina E. Pinto** is a researcher at AgroParisTech, France. She investigates whether tree species growth and survival, reveals patterns of ecological response to competition, edaphic and climatic factors, towards forest management adaptation to climatic change. **Jean-Claude Gegout** is a professor of ecology at AgroParisTech. He investigates the impact of global change on forest ecosystems and plant species distribution. **Juan Fernandez-Manjarres** is a researcher from the CNRS in France. His research is oriented towards the management of social–ecological systems and forest adaptation to climate change.

Author contributions: Y.N and J.-C.G wrote the first draft of the manuscript with important contributions from J.F-M and P.E.P-G. J.-C.G. designed the study and the experimental set-up. P.E.P.-G. performed the analyses. J-C.G. supervised the work; all authors provided critical feedback and helped shape the research and the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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