Global Change Biology

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Global Change Biology (2015) **21**, 882–896, doi: 10.1111/gcb.12683

Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shifts of two woody species

LUIS MATÍAS and ALISTAIR S. JUMP

Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK

Abstract

Ongoing changes in global climate are altering ecological conditions for many species. The consequences of such changes are typically most evident at the edge of the geographical distribution of a species, where range expansions or contractions may occur. Current demographical status at geographical range limits can help us to predict population trends and their implications for the future distribution of the species. Thus, understanding the comparability of demographical patterns occurring along both altitudinal and latitudinal gradients would be highly informative. In this study, we analyse the differences in the demography of two woody species through altitudinal gradients at their southernmost distribution limit and the consistency of demographical patterns at the treeline across a latitudinal gradient covering the complete distribution range. We focus on *Pinus sylvestris* and *Juniperus communis*, assessing their demographical structure (density, age and mortality rate), growth, reproduction investment and damage from herbivory on 53 populations covering the upper, central and lower altitudes as well as the treeline at central latitude and northernmost and southernmost latitudinal distribution limits. For both species, populations at the lowermost altitude presented older age structure, higher mortality, decreased growth and lower reproduction when compared to the upper limit, indicating higher fitness at the treeline. This trend at the treeline was generally maintained through the latitudinal gradient, but with a decreased growth at the northern edge for both species and lower reproduction for *P. sylvestris*. However, altitudinal and latitudinal transects are not directly comparable as factors other than climate, including herbivore pressure or human management, must be taken into account if we are to understand how to infer latitudinal processes from altitudinal data.

Keywords: altitude, climate change, distribution, *Juniperus communis*, latitude, *Pinus sylvestris*, temperature

Received 22 May 2014 and accepted 6 July 2014

Introduction

Plant species do not show global distributions but are restricted to geographical ranges where the particular suites of biotic and abiotic conditions allow them to grow and reproduce (Woodward, 1987). Rapid changes in climate are predicted to disrupt these conditions, with the most dramatic effects predicted to occur at species range edges. Changes in plant phenology (Parmesan & Yohe, 2003; Menzel *et al.*, 2006; Gordo & Sanz, 2010), growth (Nemani *et al.*, 2003), or ecological interactions (Hughes, 2000; Suttle *et al.*, 2007) have been recently described as a consequence of climatic change. At the population level, such changes induce range shifts, with significant consequences for plant community structure and function and the conservation of endangered species (Parmesan & Yohe, 2003; Lovejoy & Hannah, 2005; Parmesan, 2006; Walther, 2010).

Species range changes occur via one of the most obvious biotic responses to climatic change, the migration of species to new areas as conditions become favourable to maintain populations (Jump & Peñuelas, 2005; Lenoir *et al.*, 2008). However, ranges are also likely to contract at the retreating edge of the distribution where the adverse conditions that exceed critical conditions for growth and/or reproduction become more frequent. In long-lived woody species, death is a nonlinear threshold process, so there may be little obvious evidence of decline until critical thresholds are reached, potentially resulting in widespread dieback with major consequences for ecosystem structure and function (van Mantgem & Stephenson, 2007; Allen *et al.*, 2010). As a consequence of these variations, it is possible to distinguish three different types of range alteration in response to climate (Hampe & Petit, 2005): (i) range expansion, when the leading edge of the distribution is advancing into newly favourable regions but no changes appear at the trailing edge; (ii) range contraction, when only trailing edge populations decline with no alteration of the leading edge and (iii) range

Correspondence: Luis Matías, tel. + 44 1786 467757, fax + 44 01786 467843, e-mail: luis.matiasresina@stir.ac.uk

displacement, when both leading and trailing edges move upward or poleward.

Studies analysing species performance across climate gradients, i.e. covering wide altitudinal or latitudinal ranges, can provide invaluable information about the consequences of climate variation on ecosystem function and dynamics (De Frenne *et al.*, 2013). Although there is an increasing number of studies identifying range shifts in woody species as a consequence of recent changes to temperature and water balance (Lloyd & Fastie, 2003; Peñuelas & Boada, 2003; Harsch *et al.*, 2009; Hofgaard *et al.*, 2012), alteration of biotic interactions (Speed *et al.*, 2012) or changes in land use (Dirnböck *et al.*, 2003; Améztegui *et al.*, 2010), published studies are heavily biased towards upward and poleward expansions, while less attention has been paid to range retractions of the equatorial and lower altitudinal range edge (but see Jump *et al.*, 2006; Bertrand *et al.*, 2011; Zhu *et al.*, 2012 or Benavides *et al.*, 2013). One of the main reasons for this bias in literature is the disparity between the rapid establishment increase at the leading edge of the distribution as climatic conditions become favourable for seed production and seedling establishment (colonisation credit; Jackson & Sax, 2009) and the persistence of relict populations at the trailing edge of the distribution even when the conditions are no longer favourable (Jump *et al.*, 2009; Hampe & Jump, 2011), otherwise known as extinction debt (Hanski & Ovaskainen, 2002; Jackson & Sax, 2009). Thus, range retractions are more likely to remain undetected than range expansions even though significant changes to population demography may be occurring. Studies encompassing the entire range of a species, or at least the northern and southern (or lower and upper) extremes, are scarce (Parmesan, 2006), mainly because of the difficulties of gathering data on the scale of a species' range, often covering much of a continent. However, it is necessary to consider the complete altitudinal and latitudinal distribution range for an accurate prediction of climate-change consequences on species' distribution, given the different biotic and abiotic processes occurring along both types of geographical gradients (Jump *et al.*, 2009; De Frenne *et al.*, 2013; Lenoir & Svenning, 2014).

At both altitudinal and latitudinal limits, population expansion at the leading edge depends on the specific migration potential of the population by seed production, effective dispersal (long-distance dispersal) and seedling establishment, and by the growth capacity of individuals and of the population (Hampe & Petit, 2005; Lapenis *et al.*, 2005). If the leading edge is expanding, populations should be characterised by a demographical structure that displays proportionately more seedlings and saplings and hence relatively fewer old individuals. On the contrary, if the distribution range is contracting at the trailing edge, populations should be characterised by an older mean age of individuals due to proportionately more old individuals and fewer seedlings and saplings due to rare recruitment, as well as by diminished growth and reproduction investment. For long-lived organisms, demographical trends of trailing edge populations cannot simply be inferred from their current recruitment or growth rates since existing adults still contribute to rare recruitment events when conditions allow (e.g. Eriksson, 1996). Consequently, changes of adult mortalities must also be considered as indicators, but these have scarcely been monitored (but see van Mantgem & Stephenson, 2007). Furthermore, population genetic structure typically differs between trailing edge and core populations. The small size and greater isolation of trailing edge populations being associated with their greater divergence with respect to the core of the species distribution (Hampe & Petit, 2005), although the potential feedbacks of genetic structure to demography are scarcely understood.

To determine the consequences of the rise in global temperatures recorded during the last decades on species' range limits, we sampled populations across altitudinal and latitudinal gradients, covering the uppermost/lowermost and northernmost/southernmost limits of the distribution of two widespread woody plant species: the Scots pine (*Pinus sylvestris* L.) and the common juniper (*Juniperus communis* L.). We aimed to determine the geographical variation in components of population performance (namely demographical structure, secondary growth, reproductive investment and biotic interactions) and identify their implications for potential altitudinal and latitudinal range shifts.

Materials and methods

Focal species and study areas

Scots pine (*P. sylvestris* L.) and common juniper (*J. communis* L.) are long-lived gymnosperms representing two different plant functional groups (trees and shrubs respectively) and dispersal types (anemochorous and zoochorous respectively). These two species have expanded and contracted their ranges several times during the glacial and interglacial periods, and currently they share a common distribution range, being among the most widely distributed woody species in the Holarctic and ranging from the Arctic to Mediterranean basin (Carlisle & Brown, 1968; García *et al.*, 2000; Thomas *et al.*, 2007; Matías & Jump, 2012). In many mountain areas, *P. sylvestris* forms the upper treeline, and *J. communis* is one of the major species in the shrubland areas above it (García *et al.*, 2000). These forests and shrublands have a high ecological value, mainly in relation to their soil-retaining ability, their associated endemic flora and fauna, and their traditional use as summer grazing areas (Carlisle & Brown, 1968). From an economic point of view, *P. sylvestris* is found in all member states of the EU, where it constitutes approximately 20% of the commercial forest area, and it is of considerable importance as a timber producing species, particularly in Nordic countries (Masón & Alía, 2000). Various different varieties and subspecies have been described for the two focal species (up to 30 for *J. communis* and 5 for *P. sylvestris*; Adams, 2004; Farjon, 2005). However, we centred our sampling at species level because of the wide geographical extent of the studied range, and the geographical basis of many subspecific divisions in the taxonomy of these two species.

For each species, we selected populations along altitudinal and latitudinal gradients. The altitudinal gradient was located at the southern limit of these species in the Penibaetic Range, SE Spain (Table 1). Five different populations were selected for *P. sylvestris* and six for *J. communis* (mean size 3.9 ± 0.3 ha) in each of the three altitudinal bands: lowermost limit (possible contraction area), core of the distribution and uppermost limit (possible expansion area; Fig. 1a), covering the whole altitudinal range. For the comparison across the latitudinal distribution range, we selected treeline populations across Western Europe. We used the same populations at the upper limit from the altitudinal range as the southernmost populations and five additional populations per species at central latitude (Cairngorms, UK), and five at the northernmost limit of the distribution (Kevo, Finland; Fig. 1b), making a total of 53 study populations. In all of them, either *P. sylvestris* or *J. communis* was the dominant species. The altitudinal gradient was not replicated in latitude since altitudinal distribution decreases with increasing latitude, presenting a very narrow altitudinal range at the northern limit of the focal species. To maintain comparability across sites, we selected the different populations maintaining orientation, slope and soil type as constant as possible. To minimise human management impacts as far as is practicable and sample populations of natural origin, we selected all populations within protected areas: Sierra de Baza Natural Park, Sierra Nevada and Cairngorms National Parks, and Kevo Strict Nature Reserve. Monthly climatic data series since 1960 were obtained from the nearest meteorological stations for the three latitudinal areas: Kevo Subarctic Research Station (69°45′N, 27°01′E; 80 m a.s.l., University of Turku), Braemar meteorological station (57°00′N, 3°23′W 339 m a.s.l., UK Met Office) and Narvaez meteorological station (37°25′N, 2°51′W 1364 m a.s.l., Junta de Andalucía).

Sampling design

Field sampling was carried out from April to September 2012. To have an overall view of the population structure of the two focal species at range limits, we estimated the population trends from the following variables in each population:

1. *Demographical structure* was estimated by randomly placing 15 transects of 25 m × 10 m per population separated from each other by at least 30 m. We recorded the number of

Table 1 Main characteristics (central location, elevation, mean distance among populations within each band and mean density of individuals) of the studied populations for the two focal species. Current temperature represents mean values from the last decade (2001–2010), and past temperature from the previous 40 years (1960–2000). Temperature and precipitation values are similar for both species at each location. Mean values are given ±SE

Site	Latitude	Location	Altitude	Elevation (m a.s.l.)	Distance (km)	Density (ind. ha^{-1})	Past T (°C)	Current T (°C)	ΔT (°C)	Mean P (mm)
Pinus sylvestris										
Altitudinal gradient										
Granada, Spain	Southern	37°05′22″N, 3°27′20″W	Low	1730 ± 23	38.4 ± 9.6	252 ± 45	12.1 ± 0.1	13.4 ± 0.1	1.3	655 ± 43
			Medium	1934 ± 15	38.5 ± 9.7	356 ± 54				
			Treeline	2107 ± 14	38.4 ± 9.8	324 ± 41				
Latitudinal gradient										
Cairngorms, UK	Central	57°08′50″N, 3°40′58″W	Treeline	489 ± 5	6.4 ± 1.1	392 ± 37	6.5 ± 0.1	6.9 ± 0.2	0.4	897 ± 18
Kevo, Finland	Northern	69°47′52″N, 27°03′29″E	Treeline	222 ± 3	2.9 ± 0.4	401 ± 45	−1.8 ± 0.2	−0.6 ± 0.2	1.2	415 ± 12
Juniperus communis										
Altitudinal gradient										
Granada, Spain	Southern	37°22′05″N, 2°51′26″W	Low	1877 ± 23	36.2 ± 6.8	164 ± 34				
			Medium	2019 ± 18	35.6 ± 6.9	214 ± 29				
			Treeline	2278 ± 27	36.1 ± 7.1	232 ± 21				
Latitudinal gradient										
Cairngorms, UK	Central	57°07′44″N, 3°48′48″W	Treeline	502 ± 5	6.4 ± 1.3	206 ± 19				
Kevo, Finland	Northern	69°49′20″N, 27°09′02″E	Treeline	291 ± 3	4.0 ± 0.8	181 ± 28				

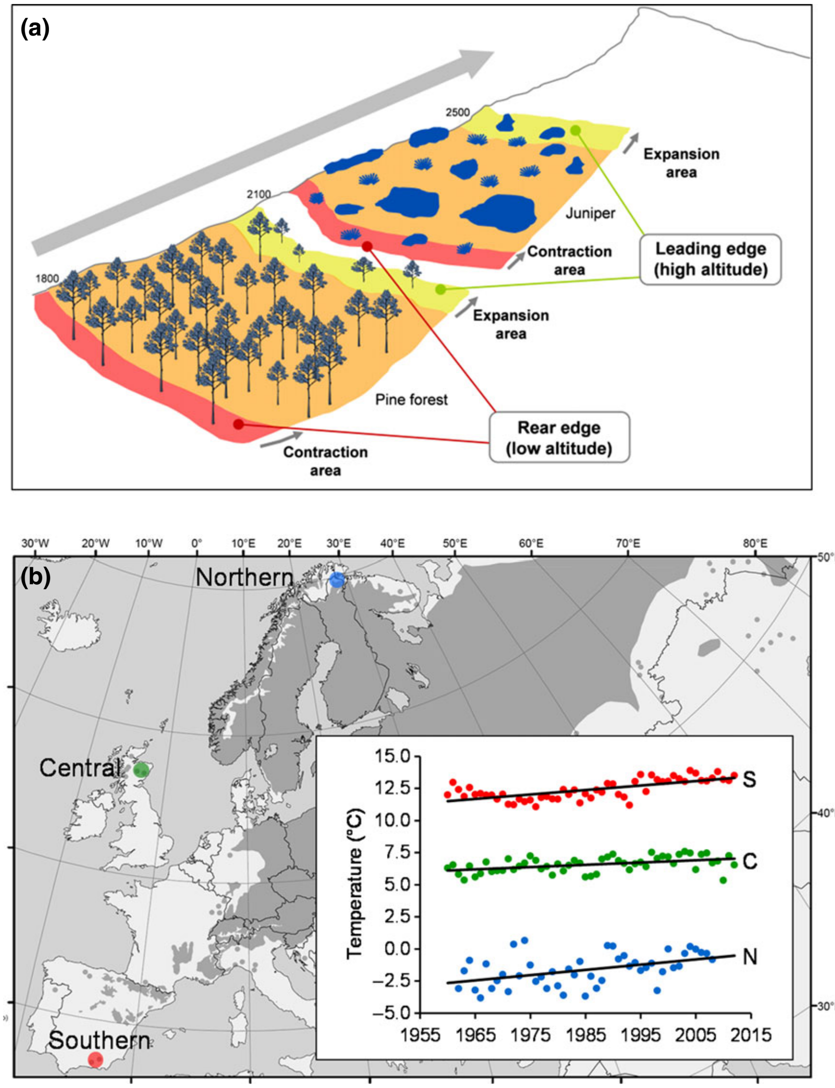

Fig. 1 Study areas across the altitudinal and latitudinal gradients investigated here. Plate (a) represents the altitudinal distribution of the two focal species at their southernmost limit, showing sampling areas at the leading edges (high altitude), core population (medium altitude) and contraction edge (low altitude). Note that while the two species coexist in altitude, they are represented separately for simplicity. Plate (b) represents the latitudinal sampled gradient, ranging from the southernmost limit (red, S. Nevada National Park and S. Baza Natural Park, Spain) to the central range (green, Cairngorms National Park, UK) and northernmost limit (blue, Kevo Strict Nature Reserve, Finland) over the European distribution of *Pinus sylvestris* (source Euforgen; http://www.euforgen.org/). The inset figure gives temperature variation during the past 50 years at the different latitudinal study areas: southern (red dots, S), $r = 0.70$, $P < 0.0001$; central (green dots, C), $r = 0.46$, $P = 0.0005$; and northern (blue dots, N), $r = 0.45$, $P = 0.0012$.

individuals, number of dead trees, diameter at breast height (DBH) and height of every individual below 2 m high for *P. sylvestris*, and number of individuals, volume (calculated as a semispheroid from maximum diameter, minimum diameter and maximum height), sex and percentage of dead biomass for *J. communis*. We used size classes (either DBH or volume) as a proxy for individual age within populations (García *et al.*, 2000). The density of individuals within size classes was used as the response variable in our analyses. A demographical structure dominated by old individuals or a high proportion of dead trees/dead biomass are indicators of recruitment failure and declining populations expected in contraction areas, whereas a evenly structured demographical distribution or dominated by young individuals may indicate a population increase, as expected in areas of range expansion (García *et al.*, 1999; Kollmann & Pflugshaupt, 2005).

2. *Secondary growth* was measured using branch increment. 15 adult individuals were randomly selected per population, avoiding individuals with significant herbivory or physical damage. Ten branches per individual were selected across all orientations, all of them between 1.5 and 2.5 m high for

P. *sylvestris* and below 1 m for *J. communis*. From each branch, yearly shoot elongation from 2007 to 2011 in *P. sylvestris* and from 2009 to 2012 in *J. communis* was recorded based on annual whorls and yearly bud scars (see Herrero & Zamora, 2014 for more details). The same proportion of male and female individuals was kept in *J. communis*. Higher growth is expected in expanding populations, whereas diminished growth relative to core populations was hypothesised for areas of potential range contraction (Hampe & Petit, 2005).

3. *Reproductive investment* was estimated as the proportion of terminal buds producing cones in *P. sylvestris*, by counting 100 buds per tree in 25 individuals per population. In the case of *J. communis*, we selected 25 female individuals per population, and counted the number of cones in five 20 cm × 20 cm sampling quadrats in each of them. Since cone maturation takes 2 years in this species, we took data from cone production in 2012 and 2013 at the same time. Expanding populations are expected to invest more resources in reproduction, whereas it is expected to be more limited in contracting ones (Hampe & Petit, 2005).
4. *Herbivory damage* was selected as a representative biotic interaction since it is common for both species, strongly important in all areas, and able to delay considerably the time to reach maturity (Zamora *et al*., 2001; Cairns & Mohen, 2004; Herrero *et al*., 2012). We estimated the accumulated herbivory damage as the proportion of apical shots browsed by ungulates with respect to the total (Herrero *et al*., 2012). All apical shots were counted in small saplings and 100 in large ones or adults. In the case of *P. sylvestris,* we used all individuals of less than 2 m height found in the demography transects and all individuals in transects for *J. communis*.

Data analysis

The effect of altitudinal or latitudinal gradients on the different response variables was explored by means of generalised linear mixed models (GLMM), using a null model with a random structure that included population as a random factor, and thus extracting the interpopulation variability from the model. In addition to the altitudinal/latitudinal responses, we also included the effect of other possible interacting variables in our models, including DBH class for demography, interannual variation in growth and reproductive investment (the latter only for *J. communis*) and height/size (for *P. sylvestris* and *J. communis* respectively) in herbivory. GLMMs were performed using Poisson distribution and log link function for the demography variables, Gaussian distribution and identity link function for growth and reproductive investment, and Binomial distribution and logit link function for herbivory. The significance of each source of variation included in these models was tested by comparing the values of their Akaike information criterion (AIC) and Schwarz's Bayesian information criterion, as well as χ^2 tests for the significance of the model (Zuur *et al*., 2009). We determined the significance of fixed factors by comparing the AICs of a model with only the intercept against the models built, including each fixed factor one at a time and in all appropriate combinations (Bates, 2011). A fixed factor significantly predicted the dependent variable when the χ^2 of the model with vs. without that factor was significant, and when the AIC of the model including that factor was lower than the AIC of the model including only the intercept. These analyses were performed separately for altitudinal and latitudinal gradients and for each species using the packages stats and lme4 in R (Bates *et al*., 2014).

Results

Mean annual temperature has raised significantly in all study areas during the past decade, with increases of between 0.4 and 1.3 °C when compared with the previous 40 years (Table 1). This trend is consistent at least since 1960 (Fig. 1), increasing 0.35 °C per decade at the southern latitude, 0.18 °C at the central latitude, and 0.41 °C at the northern limit. No significant trend in total annual precipitation was detected over the same time period for any of the study areas.

Demographical structure

For both species, the best explanatory model included DBH classes and the altitudinal or latitudinal gradient (Tables 2 and 3). Across the altitudinal gradient, both species presented a significantly lower proportion of the smaller size classes at the lowest altitude, with populations being dominated by the biggest (and presumably older) individuals. This pattern was especially evident for *J. communis* (Fig. 2). A more balanced demographical structure with a higher proportion of young individuals appeared at the medium altitude populations for both species, whereas a greater proportion of small size classes (for *P. sylvestris*) or a proportional demographical structure (for *J. communis*) was found at high altitude populations. The proportion of *P. sylvestris* dead trees differed across altitudes ($F = 7.0$; $P = 0.009$) with significantly higher mortality at the lowest populations (6.9 ± 1.9%) than in medium (0.6 ± 0.4%) or high altitude (1.4 ± 1.0%). The same pattern appeared with the proportion of dead biomass in *J. communis* individuals ($F = 6.0$; $P = 0.01$), with higher necrosis at lowland populations (10.9 ± 3.6% vs. 2.5 ± 0.6% and 1.1 ± 0.4% in medium and high altitude respectively).

When comparing the treeline populations across the latitudinal gradient, we found that the pattern of a higher proportion of saplings below 10 cm in DBH observed at the southernmost treeline for *P. sylvestris* is even more evident with increasing latitude. This was especially noticeable at the northernmost limit, where the abundance of saplings was almost double the next most numerous size class (Fig. 3). This pattern was not as clear in the case of *J. communis* at the central latitude

Table 2 Outcome of the GLMM testing the effect of altitude and latitude on *Pinus sylvestris* performance expressed on demographical structure, growth, reproductive investment and herbivory damage. The significance of each factor was found by comparing the AICs of a model with only the intercept (population) vs. models built by including each fixed factor one at a time (maintaining the random component of the complete model). The term 'Gradient' represents either altitude or latitude in the different models. Those factors that were significant are shown in bold (the model with them had a smaller AIC than alternative models without them). Population was significant according to dotplot analysis across all the dependent variables

		Demography altitude						Demography latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	2	2129.5	2134.1	−1062.7				3403.4	3408.0	−1699.7			
Density ~ Class + (1 | Population)	6	1345.1	1359.0	−666.5	792.4	4	**<0.001**	1158.7	1172.6	−573.3	2252.6	4	**<0.001**
Density ~ Gradient + (Gradient | Pop.)	9	2139.4	2160.2	−1060.7	0.0	3	1	3414.7	3435.5	−1698.3	0.0	3	1
Density ~ Gradient * Class+(Gradient | Pop.)	21	916.0	964.7	−473.0	1247.3	12	**<0.001**	679.4	728.1	−318.7	2759.3	12	**<0.001**

		Growth altitude						Growth latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	3	69 781	69 801	−34 887				65 147	65 168	−32 571			
Growth ~ Year + (1 | Pop.)	4	69 778	69 806	−34 885	4.6	1	**0.03**	65 012	65 040	−32 502	137.2	1	**<0.001**
Growth ~ Gradient + (Gradient | Pop.)	10	69 786	69 855	−34 883	4.2	6	0.65	65 125	65 195	−32 553	0.00	6	1
Growth ~ Gradient * Year + (Gradient | Pop.)	13	69 773	69 863	−34 873	19.2	3	**<0.001**	64 922	65 012	−32 448	209.9	3	**<0.001**

		Reproduction altitude						Reproduction latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	3	2038.5	2050.3	−1016.3				1919.0	1930.8	−956.5			
Reproduction ~ Gradient + (Gradient | Pop.)	10	2021.8	2061.1	−1000.9	30.7	7	**<0.001**	1918.5	1957.7	−949.2	14.6	7	**0.041**

		Herbivory altitude						Herbivory latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	2	9429.0	9436.9	−4712.5				11 508	11 518	−5752.1			
Herb ~ Height + (1 | Pop.)	3	8973.9	8985.7	−4484.0	457.1	1	**<0.001**	11 409	11 423	−5701.3	101.5	1	**<0.001**
Herb ~ Gradient + (Gradient | Pop.)	9	9431.0	9466.6	−4706.5	0.0	6	1	11 499	11 541	−5740.3	0.0	6	1
Herb ~ Gradient * Height + (Gradient | Pop.)	12	8778.7	8825.7	−4377.4	658.3	3	**<0.001**	11 384	11 440	−5679.8	121.0	3	**<0.001**

GLMM, generalised linear mixed models; AIC, Akaike information criterion; BIC, Bayesian information criterion.

Table 3 Outcome of the GLMM testing the effect of altitude and latitude on *Juniperus communis* performance expressed on demographical structure, growth, reproductive investment and herbivory damage. The significance of each factor was found by comparing the AICs of a model with only the intercept (population) vs. models built by including each fixed factor one at a time (maintaining the random component of the complete model). The term 'Gradient' represents either altitude or latitude in the different models. Those factors that were significant are shown in bold (the model with them had a smaller AIC than alternative models without them). Population was significant according to dotplot analysis across all the dependent variables

		Demography altitude						Demography latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	2	1825.1	1830.8	−910.6				1166.0	1171.6	−581.0			
D ~ Class + (1 ∣ Population)	9	1011.7	1037.3	−496.9	825.8	0	**<0.001**	863.6	888.8	−422.8	312.9	0	**<0.001**
D ~ Gradient + (Gradient ∣ Pop.)	9	1837.5	1836.1	−909.8	1.6	7	0.979	1176.5	1201.7	−579.3	3.5	7	0.833
D ~ Gradient * Class + (Gradient ∣ Pop.)	30	605.9	691.2	−272.9	447.9	21	**<0.001**	577.8	662.0	−258.9	327.7	21	**<0.001**

		Growth altitude						Growth latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	3	47 076	47 096	−23 535				39 559	39 579	−19 777			
Growth ~ Year + (1 ∣ Pop.)	4	47 077	47 104	−23 534	0.9	1	0.34	39 480	39 506	−19 736	81.2	1	**<0.001**
Growth ~ Gradient + (Gradient ∣ Pop.)	10	47 041	47 109	−23 511	47.6	6	**<0.001**	39 521	39 587	−19 761	0.0	6	1
Growth ~ Gradient * Year + (Gradient ∣ Pop.)	13	47 036	47 124	−23 505	10.9	3	**0.01**	39 378	39 464	−19 676	149.2	3	**<0.001**

		Reproduction altitude						Reproduction latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	3	4601.1	4612.8	−2297.6				4062.7	4074.0	−2028.4			
Reproduction ~ Year + (1 ∣ Pop.)	4	4602.2	4617.7	−2297.1	1.0	1	0.32	4064.6	4079.6	−2028.3	0.2	1	0.66
Reproduction ~ Gradient + (Gradient ∣ Pop.)	10	4587.5	4626.3	−2283.7	26.7	6	**<0.001**	4071.3	4109.0	−2025.7	5.2	6	0.52
Reproduction ~ Gradient * Year + (Gradient ∣ Pop.)	13	4592.1	4642.6	−2283.0	1.4	3	0.70	4077.0	4126.0	−2025.5	0.4	3	0.94

		Herbivory altitude						Herbivory latitude					
Model	df	AIC	BIC	LogLik	χ^2	df	*P*	AIC	BIC	LogLik	χ^2	df	*P*
Intercept	2	5812.7	5822.4	−2904.4				11 508	11 518	−5752.1			
Herb ~ Volume + (1 ∣ Pop.)	3	5782.6	5797.0	−2888.3	32.1	1	**<0.001**	11 505	11 519	−5749.4	5.4	1	**0.019**
Herb ~ Gradient + (Gradient ∣ Pop.)	9	5821.9	5865.3	−2802.0	0.0	6	1	11 499	11 541	−5740.3	18.1	6	**0.006**
Herb ~ Gradient * Volume + (Gradient ∣ Pop.)	12	5719.3	5777.2	−2847.7	108.6	3	**<0.001**	11 397	11 453	−5686.3	108.0	3	**<0.001**

GLMM, generalised linear mixed models; AIC, Akaike information criterion; BIC, Bayesian information criterion.

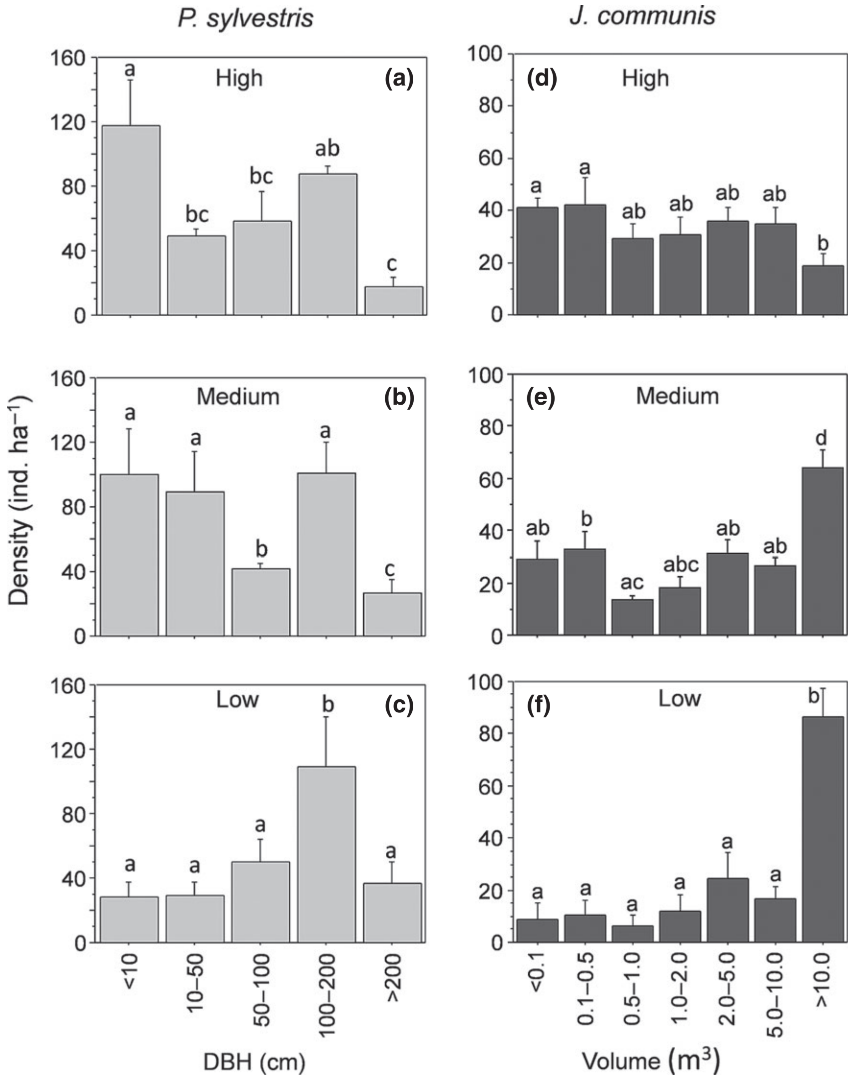

Fig. 2 Density of individuals (in individuals per hectare) for different size classes (diameter at breast height, DBH, for *Pinus sylvestris*, light grey bars, and volume for *Juniperus communis*, dark grey bars) across the altitudinal gradient (a, d: high; b, e: medium; c, f: low). Different letters denote statistically significant differences (at $P < 0.05$) among size classes. Error bars indicate standard error.

populations (although still a relatively even distribution across size classes), but it appeared again at the northernmost limit, providing evidence of high recruitment success at treeline populations across the whole latitudinal distribution range. We did not find differences in *P. sylvestris* mortality across latitude ($F = 1.36$; $P = 0.29$), and dead biomass was greater in northern populations (3.1 ± 0.6%; $F = 5.6$; $P = 0.02$) than in the other two latitudes (1.1 ± 0.4% and 0.9 ± 0.4% in southern and central latitudes respectively).

Growth

Growth differed across altitudinal and latitudinal gradients for both species (Tables 2 and 3). Across the altitudinal range, individuals from medium elevation populations grew better than at range limits (Fig. 4a). But in both species, branch increment at treeline was higher than at the lowermost limit, indicating better conditions for growth at the upper than at the lower limit. At the treeline across the latitudinal distribution range, we observed that the growth of *P. sylvestris* declined with increasing latitude (Fig. 4b), whereas growth for *J. communis* was highest in central latitude populations and lowest at the northern limit.

Reproduction

As was the case with branch growth, reproductive investment was higher at central altitude populations

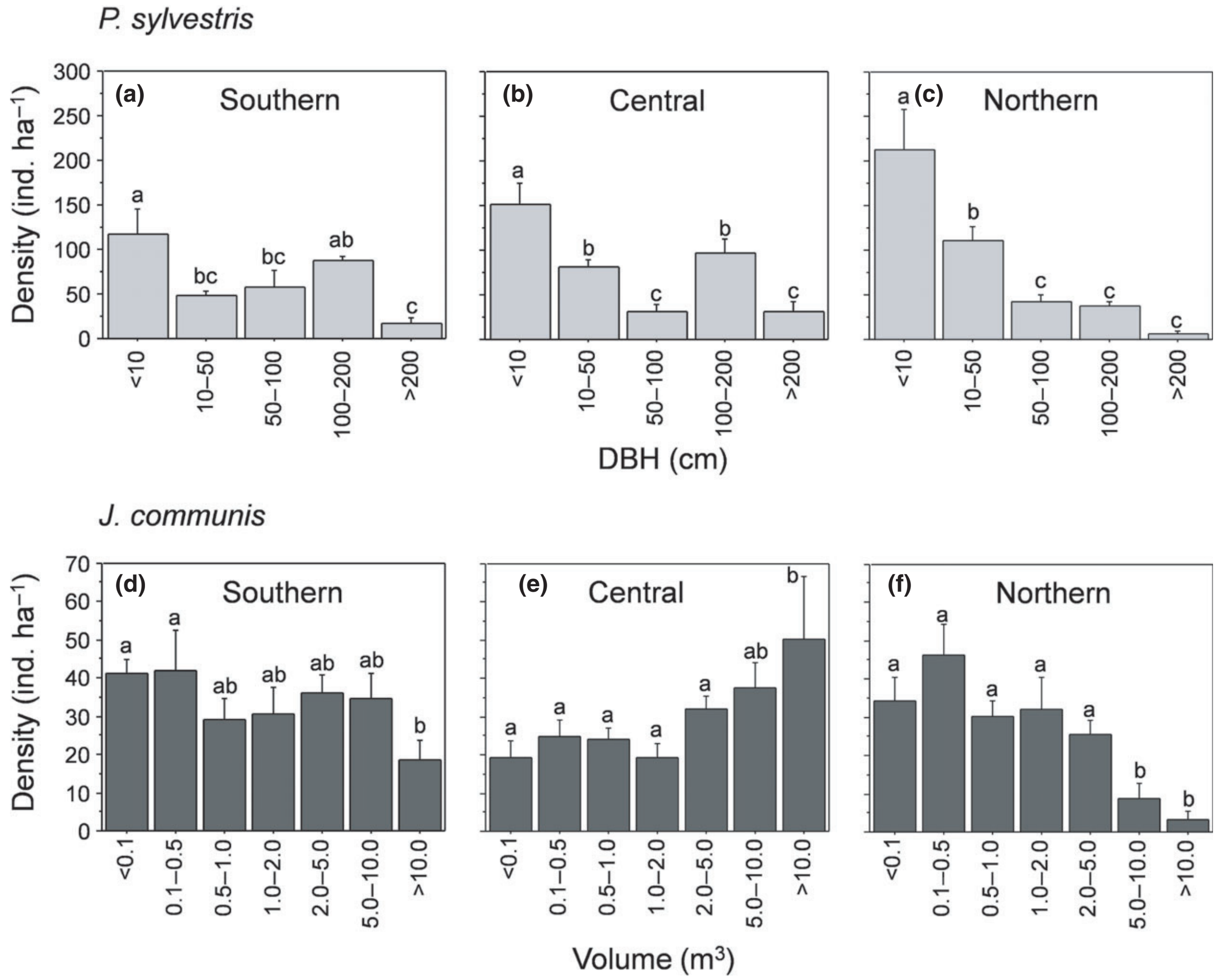

Fig. 3 Density of individuals (in individuals per hectare) for different size classes (diameter at breast height, DBH, for *Pinus sylvestris*, light grey bars, and volume for *Juniperus communis*, dark grey bars) at treeline populations across the latitudinal gradient (a, d: southern; b, e: central; c, f: northern). Letters and error bars as in Fig. 2.

than in the extremes for the two focal species but, again, it was higher at the upper limit than at the low altitude limit (Fig. 5). Through the latitudinal distribution of *P. sylvestris*, we found a trend towards reduction in reproduction as latitude increased for treeline populations, whereas cone production did not differ with latitude in the case of *J. communis*, as denoted by the lack of significance of the model including latitude (Table 3). No interannual variations were identified for *J. communis* across either the altitudinal or latitudinal gradient.

Herbivory

Damage caused by browsers on the focal species was different across both altitudinal and latitudinal gradients (Tables 2 and 3). The two species differed in the intensity of damage recorded, *P. sylvestris* having overall a higher probability of being attacked than *J. communis* (58.7% vs. 42.9% respectively) and suffering higher damage once attacked (43.7% vs. 10.6%). With altitude, herbivore pressure was more intense at the lower limit for *P. sylvestris*, whereas *J. communis* was mainly consumed at the treeline (Fig. 6). There were also differences across the latitudinal distribution of the species. *P. sylvestris* had a much higher herbivore pressure at the southern range than at any other latitude (87.5% of individuals were consumed), whereas the highest damage was found in central latitude populations for *J. communis*. Consequently, there was no identifiable common pattern for herbivory across the altitudinal or latitudinal gradients.

Discussion

In this study, we present the results of a field sampling that assessed the latitudinal and altitudinal distributions

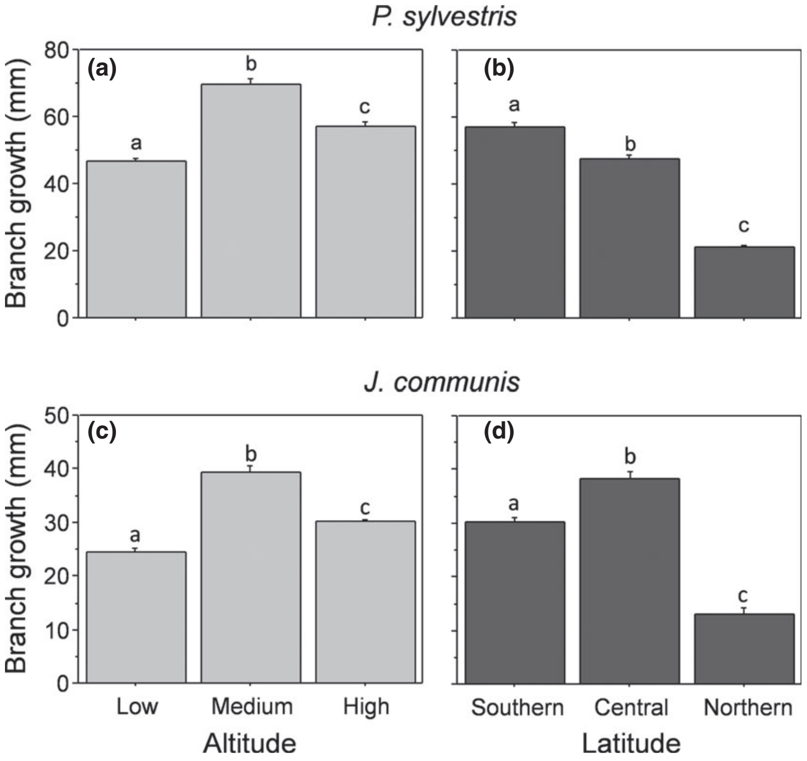

Fig. 4 Secondary growth (mean values for 2007–2011 for *Pinus sylvestris* and 2009–2012 for *Juniperus communis*), estimated as branch elongation for the two focal species (a, b, *P. sylvestris*; c, d, *J. communis*) across the altitudinal gradient (light grey bars) and latitudinal gradient (dark grey). Letters and error bars as in Fig. 2.

of two woody species. We found evidence for both future population expansions at high altitudinal and latitudinal limits and a trend towards population decline at the lowest part of the species' southern edge. Our results suggest a potential for an impending range shift, in agreement with the observed rise in mean temperature across the study areas.

Altitudinal variation

We found that the demographical structure of both *P. sylvestris* and *J. communis* populations differs across the altitudinal distribution at their southernmost limit. When compared with the central altitude, both species presented a significantly reduced proportion of young individuals at the lowermost populations, and a clear dominance of older age classes. Although this decreased recruitment at the lowest end of the altitudinal distribution is common for many woody species (Gworek *et al.*, 2007; Lenoir *et al.*, 2009; Rabasa *et al.*, 2013), it clearly contrasts with the pattern found at the treeline, where we identified a higher proportion of saplings or an even distribution across age classes. In addition, there was higher mortality (quantified as either trees or biomass) in the lowest populations than at the other altitudes. These results are consistent for both species with lower growth rate and decreased reproductive investment, indicating a potential for population decline of the lowest altitude populations.

Although we did not find a significant reduction in precipitation in this area during the last decades, the observed temperature increase induces higher water loss from both soil and leaves, enhancing the already high drought stress during summer in Mediterranean mountains (Castro *et al.*, 2004; Matías *et al.*, 2012), and declining vitality at individual and population level (Linares *et al.*, 2009, 2012). This reduced tree health can predispose populations to pest and pathogen outbreaks and can exacerbate the damage that such outbreaks or extreme drought events cause (Allen & Breshears, 1998; Dobbertin *et al.*, 2005), potentially resulting in massive mortality events (Allen *et al.*, 2010). On the other hand, higher temperatures reduce the cold limitation and frost damage at the treeline, allow better growth and higher cone production, causing population expansion beyond the current limits.

The recruitment failure at the lowest edge, together with the higher proportion of dead trees or dead biomass, and the lower growth and reproductive investment all suggest a rapid decline of the lowest

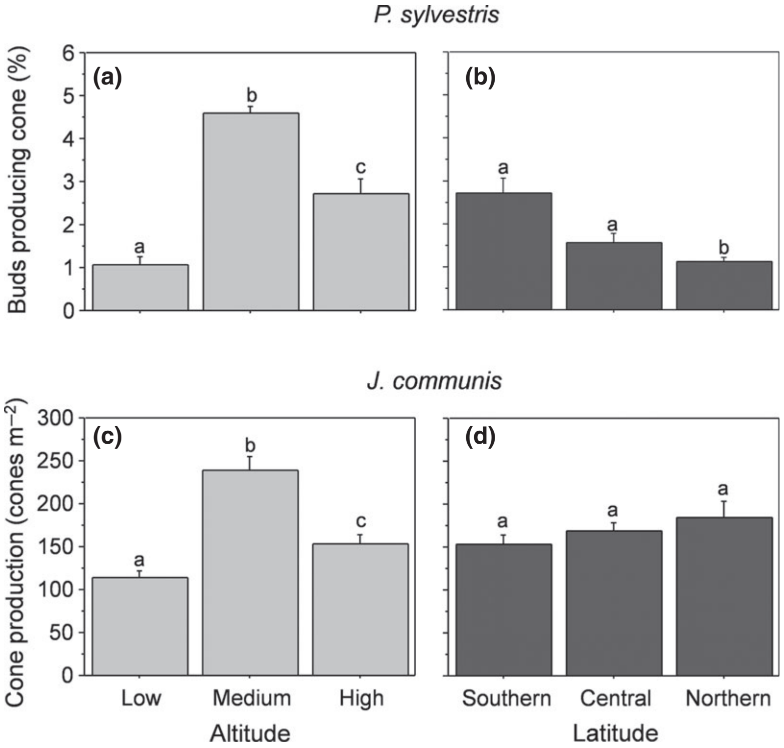

Fig. 5 Reproductive investment, estimated as the proportion of buds producing cone for *Pinus sylvestris* and as the number of cones per surface area for *Juniperus communis*, for the two focal species (a, b, *P. sylvestris*; c, d, *J. communis*) across the altitudinal gradient (light grey bars) and latitudinal gradient (dark grey). Letters and error bars as in Fig. 2.

populations is in process at the low altitude edge of the species, whereas evidence for treeline expansion appeared at the upper limit. These results indicate an ongoing altitudinal displacement for both species at the southernmost edge of the distribution. Although upward migration of *P. sylvestris* has been noted in other areas (Kullman, 2002; Kullman & Öberg, 2009; Holtmeier & Broll, 2011), evidence for lowland contractions in this and other woody species is scarce due to generally high individual longevity and relatively slow decline until survival thresholds are exceeded, especially for slow-growing species as *J. communis* (but see Zhu *et al.*, 2012).

Latitudinal treeline advance

The detected DBH structure at the treeline at the southern limit was overall maintained throughout the studied latitudinal gradient, with a higher proportion of younger individuals than any other size class, being especially evident at the northernmost limit for both species. Such a pattern is evidence of a range expansion across the species' distribution as a response to the reduction in cold limitation. The only exception was *J. communis* in central latitude populations, potentially because the temperature increment in this area during last decade has been lower than at the geographical extremes (0.4 °C vs. 1.2 °C and 1.3 °C at northern and southern limits respectively). However, we found a decrease in growth and reproduction at the highest altitudes with increasing latitude for *P. sylvestris*, and a growth reduction at the northern limit for *J. communis*. This is unsurprising since both processes are mainly determined by temperature (Hofgaard, 1993; Despland & Houle, 1997; Mäkinen *et al.*, 2000; Kullman, 2007). In any case, although we do not present any temporal trend for the focal species, there is evidence for increased growth and reproduction during last decade at the northern limit (Juntunen & Neuvonen, 2006; Salminen & Jalkanen, 2007; Mathisen & Hofgaard, 2011), and the results presented here do not suggest that northern expansion is limited by seed availability, especially for *J. communis*. However, we must note that only cone production was recorded in this study, and seed viability is an important feature with high variation across the latitudinal gradient studied here (García *et al.*, 2000).

Implications for latitudinal shift

Although it is not the primary objective of this research, results here presented from the southern-low

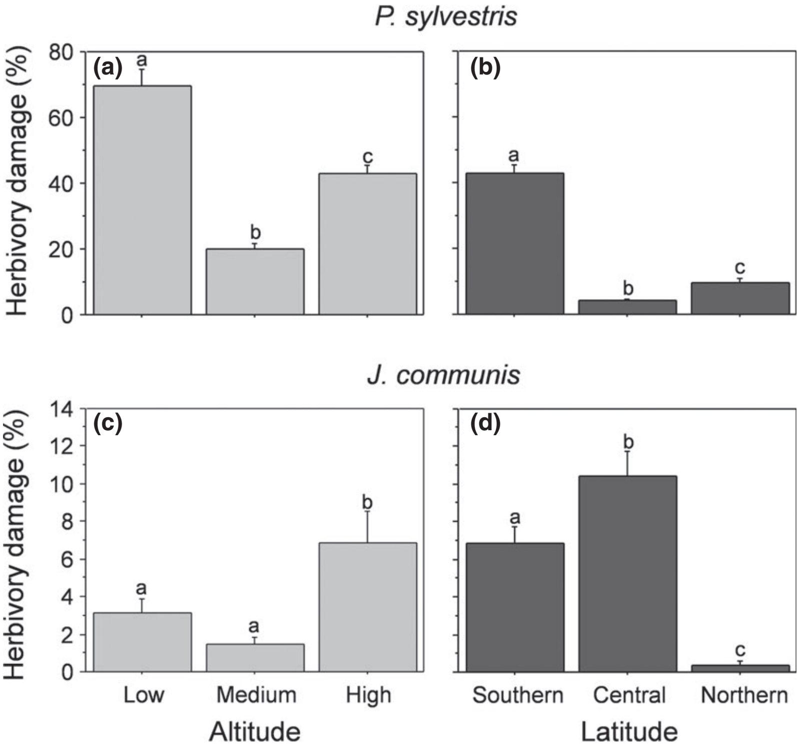

Fig. 6 Herbivory damage, measured as the proportion of consumed buds to the total, for the two focal species (a, b, *Pinus sylvestris*; c, d, *Juniperus communis*) across the altitudinal gradient (light grey bars) and latitudinal gradient (dark grey). Letters and error bars as in Fig. 2.

altitude and northern latitudinal limit give us some insights about the potential for latitudinal range alterations. As our results suggest, low altitude populations at the southern edge of the distribution are strongly susceptible to decline through a gradual reduction in population health by means of reduced growth, seed production and regeneration. The expected drought increase for the coming decades at the southern range of these species can completely hamper recruitment (Matías *et al*., 2011, 2012), which together with the low seed viability (García *et al*., 2000), and the already detected mortality increase (Vilà-Cabrera *et al*., 2013), is highly likely to result in a progressive reduction in the area occupied by these species in the Mediterranean region. This reduction in population density is predicted to result in a complex network of increasingly fragmented populations in upland areas and in those places with topographical and microclimatic conditions suitable to maintain species persistence (Jump *et al*., 2009; Hampe & Jump, 2011), as is currently the case in the studied southernmost populations for both species, and making it extensive for other southern areas. In the long-term, this patchy population structure increases the probability of nonclimate threats such as genetic drift and inbreeding or the higher consequences of catastrophic events as fires or pest outbreaks due to the lower population size. On the contrary, the registered amelioration of the limiting factors for population expansion at the coldest limit together with the demographical trends from the northernmost population presented here provide some evidence of a progressive poleward advance. In combination, these data indicate a latitudinal range displacement of the species distribution in concordance with the registered temperature rise.

However, recent experimental evidence points to the existence of local adaptation of *P. sylvestris* to drought in its southernmost populations. A controlled conditions experimental study comparing the response of *P. sylvestris* seedlings from both latitudinal extremes to the forecasted changes in temperature and precipitation provides support for a hypothesised range expansion at the northern limit on the coming decades due to a diminished growth limitation and a reduction in survival at the southern limit under forecast climate (Matías & Jump, 2014). These experimental results broadly confirm the field based research reported here. However, we also detected other factors able to modulate the general declining trend at the southern limit, such as an early seedling emergence in response to higher temperature or a higher biomass allocation to roots in plants from the southern edge (Matías & Jump, 2014; Matías *et al.*, 2014), which can increase the resistance to stress and resilience of southern-edge populations (Herrero & Zamora, 2014). The importance of varietal and subspecific structuring across the wide distribution range of these species should be considered in future work, since it might modify species-level predictions of their response to climatic alterations. For *J. communis*, persistence by longevity has been considered as an alternative to regeneration by seeding under high levels of abiotic stress (García & Zamora, 2003), and this should also be considered for predictive models.

Although we found an overall similar pattern across altitudinal and latitudinal gradients, there are important contrasts of the biotic and abiotic factors operating across altitudinal and latitudinal gradients that prevent the generalisation of the detected patterns from one gradient to the other, such as differences in atmospheric pressure, solar radiation, temperature or the strong variations in seasonal changes in photoperiod that occur across latitudes (Körner, 2007). Since the spatial distance that species should cover to maintain a similar temperature under a climate-change scenario is much greater in latitude than in altitude, we could expect longer periods to detect latitudinal range variations or community shifts (Jump *et al.*, 2009; Bertrand *et al.*, 2011). Moreover, the smaller distances along altitudinal gradients facilitate higher interpopulation gene flow, with the potential for differential patterns of local adaptations across altitudes and latitudes (Jump & Peñuelas, 2005; Jump *et al.*, 2009). Thus, altitudinal and latitudinal gradients differ in a number of critical factors that could be responsible for divergent species responses observed across both types of spatial gradients (De Frenne *et al.*, 2013). In consequence, for a proper understanding of ecological patterns across wide geographical gradients it is essential to explicitly take into account nested sampling designs where incorporating both altitudinal and latitudinal gradients.

Importance of nonclimate factors

Besides the consistent climatic effect on population demography, growth and reproduction for both species across geographical gradients, other nonclimatic factors such as biotic interactions, ecological disturbances, land use change or management practices might enhance or cancel out these trends (reviewed by Matías & Jump, 2012). Here we analysed the effects of ungulate browsing as an example of biotic interactions, due to its importance for the regeneration of woody species (Cairns & Mohen, 2004; Herrero *et al.*, 2012). At the southern edge, the strong herbivory pressure we detected on *P. sylvestris* at the lower limit could enhance the declining trend induced by climate, speeding up an altitudinal displacement or range contraction. In contrast, browsers might reduce the *J. communis* advance at the upper limit due to the higher herbivory pressure there, as reported by Speed *et al.* (2012). The biotic interactions of these species are, therefore, strongly contrasting unlike the concordant changes in growth and reproduction. It has been suggested that biotic interactions are less prevalent at higher latitudes (Schemske *et al.*, 2009), and this seems to be the case for browsing, at least at the northern limit of the distribution. These differences across species and geographical areas are due to the differential browser species (deer, ibex, moose, reindeer or domestic livestock) and land management, and strongly vary across the species' distribution. In lowland areas, interaction with other woody species is also very important, since competitors such as sclerophyllous oaks or shrub species, which can better tolerate higher temperature and drought might replace them over coming decades (Galiano *et al.*, 2010; Matías *et al.*, 2012). These are only some examples among the many possible biotic factors affecting range distributions, but the lack of consistency found here highlights the importance and the heterogeneity of nonclimatic factors when covering wide geographical areas. This contrasting pattern of biotic interactions between species emphasises the difficulties for generating general predictions at species range scale and for the construction of accurate models for forecasting plant responses to environmental change range-wide. Changes in land use might also have either positive or negative consequences in species range limits by the expansion of forest species to abandoned cultivated areas or by the increase in habitat fragmentation (Schröter *et al.*, 2005). In addition, many other factors as nitrogen and sulphur deposition, fire or pest outbreaks increase demographical stochasticity, altering current population trends and their response to climate variations (Honnay *et al.*, 2002; Skov & Svenning, 2004; Jump & Peñuelas, 2005; Gruwez *et al.*, 2014), as well as the interactions between biotic interactions and climate (Tylianakis *et al.*, 2008; Blois *et al.*, 2013).

Conclusions

Ongoing changes in climate across species distributions are altering their demographical structure, growth and reproductive investment. As far as we know, this is the first study explicitly analysing plant population responses to climate change across their altitudinal and latitudinal limits (but see García *et al.*, 2000). Our data suggest that range advance at the northernmost limit is evident. Although the lowland rear-edge limits of the focal species have not changed, we detected strong indicators of declining vitality in these populations, providing evidence of high vulnerability and the probability of decline in the near future. Thus, studies like this one, focused on rear-edge populations, are highly important for the early detection of threatened areas or populations to allow us to prepare and plan for the impacts of change whether on resource availability to human populations, biodiversity or other ecosystem services. The patterns presented here clearly indicate a strong potential for an imminent shift in the species range. However, factors other than climate affect the species growth and reproduction at the same time, and the result of their interactions is strongly heterogeneous across areas and species. Therefore, coordinated research across altitudinal and latitudinal gradients, and taking into account factors in addition to climate such as biotic interactions, land use or local adaptations are strongly recommended for an accurate forecasting of climate-change consequences on plant species.

Acknowledgements

We thank Regino Zamora, Seppo Neuvonen and Phil Wookey for logistic support during field sampling and valuable suggestions about sampling design and sites, M. Abdelaziz for helpful comments and A.J. Perez for Fig. 1a design. This research was funded by the projects MIGRAME (RNM6734) and by a FP-7 Marie-Curie grant (FP7-2011-IEF-300825) to LM.

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