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From the individual to the landscape and back: time-varying effects of climate and herbivory on tree sapling growth at distribution limits

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Summary

1. As herbivory can modulate climate-induced shifts in species distribution, disentangling the relative importance of herbivory and climate on plant growth can help to predict and manage future changes in vegetation, such as those occurring at treeline areas.

2. An individual-based hierarchical Bayesian time-series model (individual-based model; IBM) was developed to estimate the time-varying impact of climate and herbivory on individual pine sapling height growth in woodland and treeline ecosystems of southern Europe during a 16-year period. The performance of the IBM was compared to a linear mixed-effects (LME) model to test for potential inferential effects when individual variability is marginalized. Time-varying models were also compared to constant parameter approaches.

3. Model fitting and posterior predictive checking suggests a better statistical performance of individual-scale, time-varying inference. LME modelling overestimated herbivory effects and underestimated environmental stochastic effects, and model validation indeed suggested severe overfitting in the LME model relative to the IBM strategy. These results reveal a potential failure of common aggregation strategies to correctly resolve the effects of climate and herbivory variability at the individual scale. Moreover, ignoring the time-varying nature of the effects may preclude the correct estimation of the temporal scale of climate and herbivory impacts.

4. In general, we found stronger individual- and time-averaged effects of summer precipitation relative to the effects of herbivory, particularly at the treelines. Also, individual pine responses showed effects of the same sign more consistently in the case of precipitation. This suggests that precipitation is more pervasive at the population level, while herbivory act as a spatially aggregating force through individual-level damage.

5. *Synthesis*. Our results suggest that accounting for individual and temporal variability in ecological inference greatly improves the assessment of the relative importance of climate and herbivory on species distribution shifts. Strong effects of precipitation at the treeline could allow tree upward expansion, although increasing ungulate populations and associated browsing damages might limit positive climatic responses of pine saplings in the near future. In this context, the spatially heterogeneous effect exerted by herbivory could result in diverse vegetation structures in ecotones, adding a new dimension to the predictions on climate-driven vegetation shifts.

Key-words: browsing, height growth, hierarchical Bayesian models, individual heterogeneity, long-term studies, *Pinus* sp., plant population and community dynamics, precipitation, red deer, treeline

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Introduction

Climate and herbivory, as bottom-up and top-down forces, respectively, are among the main factors influencing the distribution, performance and abundance of plant species (Davidson 1993; Archibold 1994; Speed *et al.* 2010). Under the current climate change scenario, fast distributional shifts of species are expected in response to increasing warmer conditions (Parmesan & Yohe 2003; Harsch *et al.* 2009; Matías & Jump 2015). Herbivory can modulate such changes, inhibiting or exacerbating plant responses to climate. Lower herbivory pressure could favour upward expansions of woody plant species associated with climate (Sanz-Elorza *et al.* 2003; Cairns & Moen 2004). However, the role of herbivores in changing tree and shrub distributions generally opposes that of climate warming; whereas warmer temperatures facilitate the spread of trees and shrubs to higher latitudes and altitudes, high densities of herbivores can constrain upward and northward movements (Post & Pedersen 2008; Olofsson *et al.* 2009; Speed *et al.* 2010; Kaarlejärvi, Hoset & Olofsson 2015). Changes in herbivore density are thus likely to contribute to shifts in community composition in addition to, and possibly in interaction with, the better-studied climatic drivers. Therefore, disentangling the relative importance of climate and herbivory on plant performance can help to forecast species distributional changes and improve our understanding of the complex interplay between climate and biotic interactions. In addition, insights into the interactions between herbivores and climate, as drivers of shifts in community composition, have the potential for facilitating the management of herbivore populations to buffer the effect of global warming on distribution shifts in alpine plant communities.

Traditionally, the effects of climate and herbivory have been analysed at the population or landscape level through the aggregation of individual-level data. However, aggregation over the individual scale to higher scales can degrade information and hide individual characteristics not apparent from group-level attributes (Clark 2010; Clark *et al.* 2011a). Recent studies using disaggregated individual data have shown the importance of individual-level variation. In fact, this variation allows species to differ in their distributions of responses to the environment, although populations might not differ on average, playing an important role in species coexistence in forest ecosystems (Clark *et al.* 2007; Clark 2010). The individual scale has also been considered in studies assessing vulnerability of tree species to climate change, demonstrating its importance in plant performance (Clark *et al.* 2012). These approaches can be framed within the ecological (or aggregate) inference problem, which aims at drawing conclusions about individual-level behaviour from aggregate-level data (Schuessler 1999). It is well known that the marginalization of individual-level data on statistical summaries or aggregates degrades statistical inference by biasing the estimates of ecological regression parameters to the group average (see Robinson 1950; Hammond 1973; Gelman *et al.* 2001). Thus, the analysis of climate and herbivory impact at the individual level could provide new insights into the understanding of the interplay between climate and biotic interactions.

The goal of this study was to analyse the tree sapling height growth response to climate and herbivory in Mediterranean pinewoods at the individual and population levels. Height growth is related to reproductive age in pine saplings, which represent the near future of the forest (Zamora *et al.* 2001; Herrero *et al.* 2012). This is especially relevant at species distribution leading edge such treelines, where climate-driven range expansions can occur and populations are composed mainly of young individuals (Matías & Jump 2012, 2015). The study was performed at the southernmost distribution limit of two widespread species (*Pinus sylvestris* L. and *P. nigra* Arnold), considering woodland as well as treeline areas to test whether pine saplings respond differently to climate and herbivory at their altitudinal margin and to detect the potential for upward migration. Both climate and herbivory can severely constrain height growth in Mediterranean areas, especially at species southern distribution limits (Hampe & Petit 2005; Herrero *et al.* 2012), hampering upward migrations at the treeline. Thus, disentangling the relative effects of climate and herbivory in height growth can help to detect species range shifts and to assess future viability of tree populations under the current climate change scenario.

Climate fluctuations, saplings height growth, herbivory damage and the number of ungulates were monitored for 16 years. This period of time is sufficient to properly analyse demographic dynamics of a sapling cohort, as both *P. sylvestris* and *P. nigra* are able to reach maturity in 12–15 years (Debain *et al.* 2007; Boulant *et al.* 2008). Thus, plant performance was analysed over the entire life span of target saplings, prior to adult reproductive phase, the sapling phase being a key ontogenetic stage for forest expansion. We use an individual-based hierarchical Bayesian time-series model (hereafter Individual-Based Model; IBM) to estimate the effects of climate and herbivory on the temporal dynamics of pine sapling height growth at the individual level. Bayesian hierarchical modelling allows the optimal structuring of different sources of uncertainty and heterogeneity arising from the process, parameters and data levels of ecological models (Cressie *et al.* 2009). Given that we are dealing with an ontogenetic process, our IBM approach explicitly incorporate a time-varying modelling scheme for estimating the possibly shifting effects of herbivory and precipitation on tree sapling growth across time (see Carrer 2011 for a similar approach). In addition, the effects of climate and herbivory on plant growth were also modelled using a standard linear mixed-effects (hereafter LME) model, where individual-level data were aggregated at the population level (e.g. Speed *et al.* 2011a; Martínez-Vilalta *et al.* 2012). This will allow us to test for the potential inferential effects of aggregation at the individual scale (Clark *et al.* 2011a). Finally, time-varying approaches were also compared to constant parameter approaches for both IBM and LME models to assess the influence of temporal variability in the estimated effects.

In summary, the aims of this study were as follows: (i) to test for the relative importance of climate and herbivory in pine sapling height growth trends at the individual (IBM) and population level (LME); and (ii) to compare the effect of climate and herbivory in treeline and woodland areas.

Materials and methods

STUDY SITE

The study was conducted at Sierra de Baza Natural Park (SE Spain, 2°51′48″W, 37°22′57″N). *Pinus sylvestris* and *P. nigra* populations at Sierra de Baza are among the southernmost populations of the two species (Barbéro *et al.* 1998). The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought. Precipitation is concentrated mainly in autumn and spring, with an annual rainfall of 495 ± 33 mm (mean ± SE for 1991–2006 period), and summer rainfall (months of June, July and August) of 31 ± 9 (mean ± SE for 1991–2006 period; Cortijo Narváez meteorological station, 1360 m a.s.l.). The main herbivore affecting height growth of the target species is the regional red deer (*Cervus elaphus* L.), with an approximate population of 2600 individuals in 2007 (5.04 ind km^{-2}; CMA 2009).

SAMPLING DESIGN, UNGULATE POPULATION, BROWSING DAMAGES AND PLANT PERFORMANCE

This study was conducted in two native forests (1700–2100 m a.s.l.) from 1993 to 2008. In each forest, we selected two plots (approximately 1 ha each), one in the woodland and the other at the treeline. The first forest, Boleta hereafter, is a mixed forest of *P. sylvestris* and *P. nigra* growing intermingled with an understorey composed mainly of *Juniperus communis* L., *J. sabina* L., *Berberis hispanica* L., *Astragalus granatensis* Lange and *Hormatophylla spinosa* (L.) P. Küpfer. *Pinus sylvestris* sapling density was 142 ± 24.3 and 72 ± 12.7 ind ha^{-1} in woodland and treeline, respectively; and *P. nigra* density was 88 ± 34.3 and 2 ± 2 ind ha^{-1}. Pine sapling density was measured with 10 transects of 50 m length and 10 m wide at each plot in 2008. The second forest, Fonfría hereafter, is composed exclusively of *P. sylvestris* with an understorey composed mainly by *J. communis* and *J. sabina*. Sapling density was 576 ± 91.8 and 142 ± 35.1 ind ha^{-1} for woodland and treeline, respectively. Overall, we sampled 234 pine saplings of *P. sylvestris* and *P. nigra*: 90 *P. sylvestris* and 55 *P. nigra* in Boleta woodland, 32 *P. sylvestris* in Boleta treeline, 31 *P. sylvestris* in Fonfría woodland and 26 *P. sylvestris* in Fonfría treeline. Monitored individuals were established non-reproductive saplings (older than 3 years old) at the beginning of the study.

We use red deer density data from 1993 to 2008. The data from 1993 to 2000 were extracted from Granados *et al.* (2001) and data from 2005 to 2007 from CMA (2009). Both studies used lineal transects and analysed data using DISTANCE software (Laake *et al.* 1993) and Fourier series to produce red deer density estimations. Data from 2001 to 2004 and 2008 were estimated through a state-space model (see Model construction section).

Height and browsing damage data for pine saplings were obtained in samplings performed in 1995, 1998, 2004, 2006 and 2008. All the measured saplings were tagged and mapped in the beginning of the study to enable individual identification over the study years. Tags were renewed when necessary to assure correct identification. Age was estimated as number of whorls (Edenius, Danell & Nyquist 1995) for each sapling in 1995. Beyond the measurement of height, annual internode growth (trunk elongation) and leader browsing were measured for the current year and the previous years (two previous years for the first sampling and the years needed until reach the internode measured in the previous sampling for the following samplings). Annual internode growth was measured following yearly whorls and bud scars, as both *P. sylvestris* and *P. nigra* showed one flush per year in the study area. Saplings height corresponding to previous years was estimated based on measurements of annual internode growth. Then, annual height over the period 1993–2008 was used to calculate annual relative height growth (hereafter RHG), defined as the ln-ratio between current year height and previous year height. Following Speed *et al.* (2011a), we subtracted the biological trend due to the ageing of pines with the regression model $\ln(x_{i,k,t+1}/x_{i,k,t}) = \mathrm{a}_\mathrm{k} + \mathrm{b}_\mathrm{k} \times \log_\mathrm{e}(age_{i,k,t})$, where $x_{i,k,t}$ is the height of each pine i in each plot k at time t; $\ln(x_{i,k,t+1}/x_{i,k,t})$ is thus the RHG measurement for each pine i in each plot k and time t, and $age_{i,k,t}$ is the age of each individual pine i in each plot k and time t. Parameters a_k and b_k are the regression intercept and slope, respectively, for each plot. The residuals were subtracted from this regression to obtain a standardized series of residual RHGs, hereafter rRHG. Leader browsing occurs when the terminal leader shoot of the sapling was lost to herbivory, causing a loss in the apical dominance of the pine sapling, which generally implies a reduction in height growth (as the browsed sapling need to grow in height by a lateral branch). Leader browsing of the previous years was detected by clear bifurcation or strong changes of the direction in the main stem (therefore a conservative measurement). In this context, is important to note that browsing causes more than 98% of the losses of apical dominance in *P. sylvestris* in the study area (Zamora *et al.* 2001). Measurements were made in autumn, when annual internode growth was resumed and after the main browsing period in the study area (i.e. summer). We have not detected any sapling mortality related to herbivory during the study.

MODELLING INDIVIDUAL-LEVEL RESPONSES TO CLIMATE AND HERBIVORY

Model construction

We constructed an IBM to estimate the joint time-varying effects of precipitation and herbivory on the temporal dynamics of rRHG at the individual pine level (e.g. Clark *et al.* 2010). Our approach is based on the simultaneous estimation of three linked models (see Fig. 1): a stochastic dynamics model for the red deer population at the landscape level; a model relating herbivory intensity to precipitation variability and red deer density at the plot level; and a third one modelling the individual-level response of rRHG to precipitation and herbivory intensity at the plot level.

At the upper level, the dynamics of the red deer population was modelled with a state-space approach. In a state-space model, the time series of observed population estimates is linked to the true (latent) abundances through a measurement equation, while the time series of the latent values is modelled through an ecological-process model. We used a Gompertz kernel (Dennis & Taper 1994) to model the evolution of the true population of red deer throughout the landscape,

$$n_t = n_{t-1} + r\left(1 - \frac{n_{t-1}}{K}\right) + \varepsilon_t \qquad \text{eqn 1}$$

where n_t is the $\log_e$-transformed true population size at time t, r is the intrinsic rate of increase, K the carrying capacity at the landscape

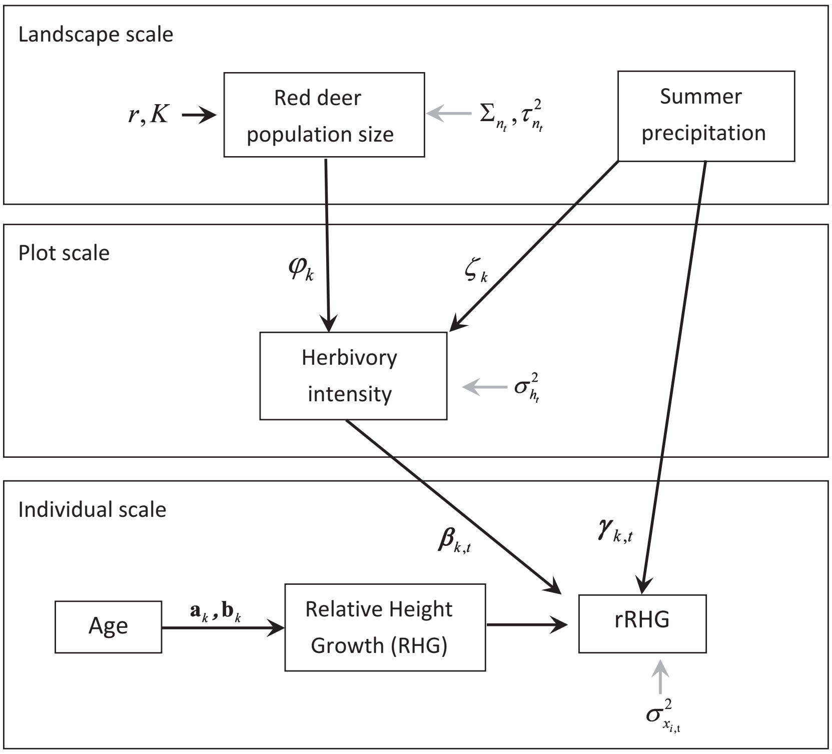

Fig. 1. A graphical representation of the individual-based hierarchical Bayesian time-series model (individual-based model; IBM) linking the dynamic variables used in the analysis, each belongs to an ecological scale. Black unidirectional arrows connecting the boxes denote a statistical effect modelled; the parameters measuring these effects are depicted along with its corresponding arrow. Grey arrows denote a stochastic effect affecting a given variable. r, K: intrinsic rate of increase and carrying capacity of red deer population, respectively; Σ_{n_t}: process variance of the stochastic term for the environmental and demographic process error of the Gompertz kernel used to model the evolution of red deer population; $\tau^2_{n_t}$: sampling variance of the Gaussian model used to link population estimates to the true abundances of red deer; φ_k, ζ_k: effects of red deer abundance and summer precipitation, respectively, on herbivory intensity (estimated as the proportion of saplings with the leader shoot browsed for each plot and species); $\sigma^2_{h_t}$: variance of the environmental noise term of the modelled herbivory intensity; $\mathbf{a}_\mathrm{k}$, $\mathbf{b}_\mathrm{k}$: the intercept and the slope, respectively, of the regression model used to subtract the biological trend in relative height growth (RHG) due to the ageing of pines; $\boldsymbol{\beta}_{k,t}$: column vector including the time-varying individual-level parameters estimating the temporal effect of herbivory on individual pines; $\boldsymbol{\gamma}_{k,t}$: column vector including the time-varying individual-level parameters estimating the temporal tracking of lagged summer precipitation by individual pines. $\sigma^2_{x_{i,t}}$: variance term for the environmental stochasticity impacting on residual RHG (rRHG). See text for further details.

level and $\boldsymbol{\varepsilon}_t$ is the stochastic term for the environmental and demographic process error. The term $\boldsymbol{\varepsilon}_t$ is sequentially independent and identically distributed noise having a normal distribution with mean 0 and variance $\Sigma_{n_t}, \varepsilon_t \sim N(0, \Sigma_{n_t})$. The matrix Σ_{n_t} is decomposed into an environmental ($\sigma^2_{n_t}$) and a demographic component (D$_t$), $\Sigma_{n_t} = \sigma^2_{n_t} + \mathbf{D}_t$, where $\sigma^2_{n_t}$ stand for the impact of environmental noise, and $\mathbf{D}_{t,}$ for the impact of demographic stochasticity. The diagonal matrix $\mathbf{D}_t = [\delta^2/\exp(n_1),\ldots, \delta^2/\exp(n_\mathrm{S})]^\mathrm{T}$ reflects the demographic variance affecting the dynamics of the red deer from time $t-1$ to t, which scales inversely with population size (e.g. Engen, Bakke & Islam 1998). Finally, the population estimates are linked to the true abundances through a Gaussian observation model,

$$y_t \sim N(n_t, \tau^2_{n_t}) \qquad \text{eqn 2}$$

where y_t is the observed red deer abundance at time t. The observation variance $\tau^2_{n_t}$ was modelled with a uniform prior distribution on the standard deviation, with a range of biologically plausible values for the red deer, $\tau_{n_t} \sim U\,(0.1,\, 0.3)$ (Daniels 2006).

At a second level, a linear regression model was fitted to estimate the effects of precipitation and red deer density on the percentage of saplings suffering leader browsing at the plot level (hereafter, herbivory intensity, denoted by $h_{k,t}$). During dry years, higher browsing damages by ungulates were recorded in the study area due to low pasture production (Zamora *et al.* 2001), indicating the potential effect of summer precipitation on leader browsing. In previous model fits we estimated the effects of precipitation and red deer density on individual-level herbivory (that is, a binomial variable expressing whether an individual was browsed or not in a given year and plot), rather than estimating these effects on herbivory intensity at the plot level. However, the convergence of parameters to a posterior distribution was unreliable in this case because many individuals in most plots never suffered an herbivory event across time, which caused an overabundance of 0s.

Prior to the analysis, summer precipitation was detrended with a linear regression of precipitation on year. Detrended summer precipitation at year t is denoted by p_t. The basic formulation of the model, for a given plot k is, then:

$$h_{k,t} = \eta_k + \varphi_k n_t + \zeta_k p_t + \varepsilon_{h_t,k,t} \qquad \text{eqn 3}$$

where η_k is the intercept, φ_k and ζ_k are the effects of red deer abundance and detrended summer precipitation on herbivory intensity ($h_{k,t}$), respectively, and $\varepsilon_{h_t,k,t}$ is sequentially independent noise distributed according to a normal distribution with mean 0 and variance $\sigma^2_{h_t}$.

At a third level, the IBM estimates the time-varying effects of precipitation and herbivory on the temporal dynamics of rRHG. We constructed separate models for each plot and species. The dynamics of the rRHG for each pine can be modelled as follows:

$$\mathrm{rRHG}_t = \mathbf{c}_k + \boldsymbol{\beta}_{k,t} h_{k,t} + \boldsymbol{\gamma}_{k,t} p_{t-1} + \boldsymbol{\varepsilon}_{x_k,t} \qquad \text{eqn 4}$$

where the column vector $\mathbf{c}_k$ contains the individual constant-level parameters of pine i at plot k, $c_{i,k}$; $\boldsymbol{\beta}_{k,t}$ is a $T \times m$ matrix including the time-varying individual-level parameters, $\beta_{i,t}$, estimating the temporal effect of herbivory on m individual pines i during T time steps, for each plot k; $\boldsymbol{\gamma}_{k,t}$ is a $T \times m$ matrix including the time-varying individual-level parameters, $\gamma_{i,t}$, which estimate the temporal tracking of detrended summer precipitation, p_{t-1}, by m individual pines i during T time steps, for each plot k. We used summer precipitation data because the effect size during these months was greater than the effect of annual precipitation, or any combinations of monthly temperatures (not shown). As conditions during bud formation strongly affect following year shoot growth in pine species such as *P. sylvestris* and *P. nigra* (Isik 1990; Dobbertin *et al.* 2010), a lagged term was used. Finally, $\boldsymbol{\varepsilon}_{x_k,t}$ is the $T \times m$ matrix including the terms for individual-level environmental stochasticity impacting on rRHG of each pine, distributed according to a normal distribution with 0 mean and a time-varying standard deviation $\sigma_{x_{i,t}}$. The temporal changes in the effects of herbivory intensity, summer precipitation and environmental stochasticity on individual rRHG were modelled through the specification of a time-varying scheme on parameters $\boldsymbol{\beta}_{k,t}$, $\boldsymbol{\gamma}_{k,t}$ and $\boldsymbol{\sigma}_{k,t}$ according to a random walk (e.g. Zeng *et al.* 1998):

$$\begin{aligned} \boldsymbol{\beta}_{k,t} &= \boldsymbol{\beta}_{k,t-1} + \varepsilon_{\boldsymbol{\beta}_{k,t},t} \\ \boldsymbol{\gamma}_{k,t} &= \boldsymbol{\gamma}_{k,t-1} + \varepsilon_{\boldsymbol{\gamma}_{k,t},t} \qquad \text{eqn 5} \\ \boldsymbol{\sigma}_{k,t} &= \boldsymbol{\sigma}_{k,t-1} + \varepsilon_{\boldsymbol{\sigma}_{k,t},t} \end{aligned}$$

where $\varepsilon_{\boldsymbol{\beta}_{k,t},t}$, $\varepsilon_{\boldsymbol{\gamma}_{k,t},t}$ and $\varepsilon_{\boldsymbol{\sigma}_{k,t},t}$ stand for the independent and identically distributed (random) noise on the red deer abundance, summer precipitation and environmental stochastic time-varying effects on individual pines, following normal distributions with 0 means and nonzero process variances $\boldsymbol{\rho}^2_{\boldsymbol{\beta}_{k,t},t}$, $\boldsymbol{\rho}^2_{\gamma_{k,t},t}$ and $\boldsymbol{\rho}^2_{\sigma_{k,t},t}$.

We decomposed the effects of summer precipitation and red deer abundance on rRHG through both direct effects of these variables and indirect effects considering the response of leader browsing to precipitation and red deer abundance (Fig. 1). Hence, a composite parameter for the down-scaled effect of red deer abundance at the landscape level on individual rRHG will be denoted by $H_{k,i,t}$; this parameter is simply the product of the effect of red deer abundance (landscape level) on herbivory intensity (plot level) and the effect of herbivory intensity on individual-level rRHG: $H_{k,i,t} = \boldsymbol{\varphi}_k \times \beta_{i,k,t}$. In the same manner, a composite parameter for the effect of summer precipitation on rRHG ($R_{k,i,t}$) can be obtained by summing the direct effect of summer precipitation on rRHG and the product of the effect of summer precipitation on herbivory intensity: $R_{k,i,t} = \boldsymbol{\gamma}_k + (\boldsymbol{\zeta}_k \times \beta_{i,k,t})$. Then, we derived population-level summary statistics to describe the collective response of the rRHG of individual pines to precipitation and herbivory at each plot studied, as well as the average environmental stochasticity at the plot level (Fig. 1). In particular, for each plot, we estimated the posterior averaged modelled effect across time within individuals and an average per plot over time and individuals (e.g. Clark *et al.* 2010). Let $\boldsymbol{\theta}_t$ stand for the averaged individual-level response to a given effect (composite herbivory or summer precipitation) at time t, or the averaged individual-level impact of environmental stochasticity. The time-varying posterior estimate for these parameters, calculated over m individuals, is derived for each plot k as:

$$\boldsymbol{\theta}_{k,t} = \frac{\sum_i^m \theta_{i,k,t}}{m-1} \qquad \text{eqn 6}$$

where $\boldsymbol{\theta}$ is a parameter of interest, $\boldsymbol{\theta} = \{\mathbf{H}_{k,t}, \mathbf{R}_{k,t}, \boldsymbol{\sigma}_{k,t}\}$. A posterior estimate of a given quantity averaged over T time steps and m individuals for each plot k is obtained as follows:

$$\boldsymbol{\theta}_k = \frac{\sum_1^T \sum_i^m \theta_{i,k,t}}{(m-1)(T-1)} \qquad \text{eqn 7}$$

Prior specification, parameter estimation and model validation

We fitted the IBM using Markov Chain Monte Carlo (MCMC) integration through Gibbs sampling. To let the likelihood dominate the prior, we placed weakly informative prior distributions on the unknown quantities. Uniform distributions were placed on the standard deviations of the environmental and demographic noise terms in the Gompertz state-space model, and in the terms for environmental and process parameter noise in eqns 3–5: σ_{n_t}, δ, σ_{h_t}, $\sigma_{x_{i,t}}$, $\rho_{\beta_{k,t},t}$, $\rho_{\gamma_{k,t},t}$, $\rho_{\sigma_{k,t},t} \sim U(0,3)$; see Gelman 2006). Note that these parameters are non-exchangeable between individuals. The location parameters, the constant-level terms and the initial values for the time-varying parameters were given flat prior normal distributions: $r, K, \eta_k, \varphi_k, \zeta_k, \mathbf{c}_k, \boldsymbol{\beta}_{k,1}, \boldsymbol{\gamma}_{k,1}, \boldsymbol{\sigma}_{k,1} \sim N(0,10)$. Note that parameters r and K were truncated at a lower level of 0 to omit biologically implausible values. We programmed the IBM in the BUGS language using the R package BRugs (R Development Core Team 2011). We ran three independent Markov Chains with dispersed initial values for 21 000 iterations and discarded the first 20 000 as a burn-in period. To increase the precision of Bayesian estimates, we merged the unthinned chains (Link & Eaton 2012). We used the R package BOA to derive the posterior estimates of parameters and latent states, and to check the convergence of the chains using standard diagnostic tests (see Gelman *et al.* 2004).

We used posterior predictive checking (Gelman *et al.* 2004) to assess the predictive ability of the fitted IBM. This is a convenient strategy for checking model adequacy (see also Clark *et al.* 2010). We used the fitted model to randomly derive through simulation 1000 synthetic time series of rRHG for each individual pine. We then plotted the average of these synthetic (posterior predicted) time series against the true value used to fit the model. The closer the synthetic data sets are to the true observations, the better the model adequacy to the focal data set (Gelman *et al.* 2004). We also used posterior predictive checks to compare the IBM in eqn 4 to the standard LME model (Speed *et al.* 2011a; Martínez-Vilalta *et al.* 2012), in which individuals are modelled as random factors and herbivory and climate variables are treated as fixed effects. This model, in which the growth of individuals is an aggregate quantity (e.g. Clark 2010), can be written as follows:

$$\mathrm{rRHG}_t = \mathbf{c}_k + \beta_{k,t} h_{k,t} + \gamma_{k,t} p_{t-1} + \varepsilon_t \qquad \text{eqn 8}$$

The time-varying parameters in the LME model are defined as unique parameters at the plot level:

$$\begin{aligned} \beta_{k,t} &= \beta_{k,t-1} + \varepsilon_{\beta_{k,t},t} \\ \gamma_{k,t} &= \gamma_{k,t-1} + \varepsilon_{\gamma_{k,t},t} \qquad \text{eqn 9} \\ \sigma_{k,t} &= \sigma_{k,t-1} + \varepsilon_{\sigma_{k,t},t} \end{aligned}$$

Note that in this model, interindividual variability is indeed allowed in the constant terms (intercepts) c_i. Again, the location parameters and the constant-level terms were given flat prior normal distributions, while uniform distributions were placed on the standard deviations of the environmental and process parameter noise (see above and see BUGS code in Appendix S2 in Supporting Information).

A critical, usually untested assumption of this modelling scheme is that individual responses are treated as stochastic realizations of a common underlying process, so that climate and herbivory are assumed to affect all individuals in a similar way. To test this assumption, posterior predicted data sets for the LME in eqn 8 were compared directly to the predictions from the IBM in eqn 4. We also used posterior predictive checking to compare the relative performance of the time-varying parameter scheme to the standard constant parameter models (e.g. Speed *et al.* 2011a; Fisichelli, Frelich & Reich 2012); in this case, the IBM with constant parameters was specified as follows:

$$\mathrm{rRHG}_t = \mathbf{c}_k + \boldsymbol{\beta}_k h_{k,t} + \gamma_k p_{t-1} + \boldsymbol{\varepsilon}_{x_k,t} \qquad \text{eqn 10}$$

and the LME models with constant parameters were specified as follows:

$$\mathrm{rRHG}_t = \mathbf{c}_k + \beta_k h_{k,t} + \gamma_k p_{t-1} + \varepsilon_t \qquad \text{eqn 11}$$

Overall, we fitted four models (IBM or LME, constant or time-varying) for each of the 4 plots and two species (20 models). For each model, we computed the proportion of variance in rRHG explained by each model (R^2) and the predicted mean squared error (PMSE) between the posterior predicted data and the true observations in both the IBM and the LME model. Finally, we calculated the deviance information criterion (DIC) for each model to compare their relative performance in terms of model complexity and fit (Spiegelhalter *et al.* 2014). The most parsimonious model will minimize this quantity. We compared model adequacy by jointly interpreting the values for R^2, PMSE and DIC.

Results

POPULATION DYNAMICS OF RED DEER AND TRENDS IN PRECIPITATION AND HERBIVORY

Figure 2c showed population dynamics of red deer during the study period. The carrying capacity of the red deer population at the landscape level (parameter K in eqn 1) was estimated at 3093.319 individuals and the intrinsic growth rate (r) at 1.125 ± 0.516. According to the fitting of the state-space Gompertz population dynamics model, 71.271% of the temporal variability in red deer abundance was driven by environmental stochastic effects, while intraspecific interactions (density dependence) accounted only for the 28.684% of this variance. Finally, the relative impact of demographic stochasticity was negligible (0.045%).

The amount of precipitation during summer declined significantly throughout the study period (Fig. 2b; $r = -0.55$, $P_{\mathrm{boot}} = 0.012$, calculated using 10 000 MC samples). By contrast, herbivory intensity (percentage of saplings displaying leader browsing) increased significantly over time in all plots ($P_{\mathrm{boot}} < 0.05$; Fig. 2d). There was large interplot variability in herbivory intensity, with very high values in Boleta woodland for *P. sylvestris* (up to 80% of browsed saplings) and relatively low values at Fonfría treeline (< 20%).

EFFECTS OF RED DEER DENSITY AND PRECIPITATION ON HERBIVORY INTENSITY

While the effect was nearly always positive, the impact of red deer population density on herbivory intensity was clearly stronger in the woodlands than in the treelines (see Table S1). In contrast, the effect of precipitation variability was generally weak.

EFFECTS OF HERBIVORY AND PRECIPITATION ON RRHG

Figure 3 shows the time-varying effects of herbivory and precipitation on rRHG in the treelines obtained with the IBM, averaged over individuals. The effect of herbivory was negligible until the end of the time series in Boleta, but was nonsignificant in Fonfría throughout the time series. In contrast,

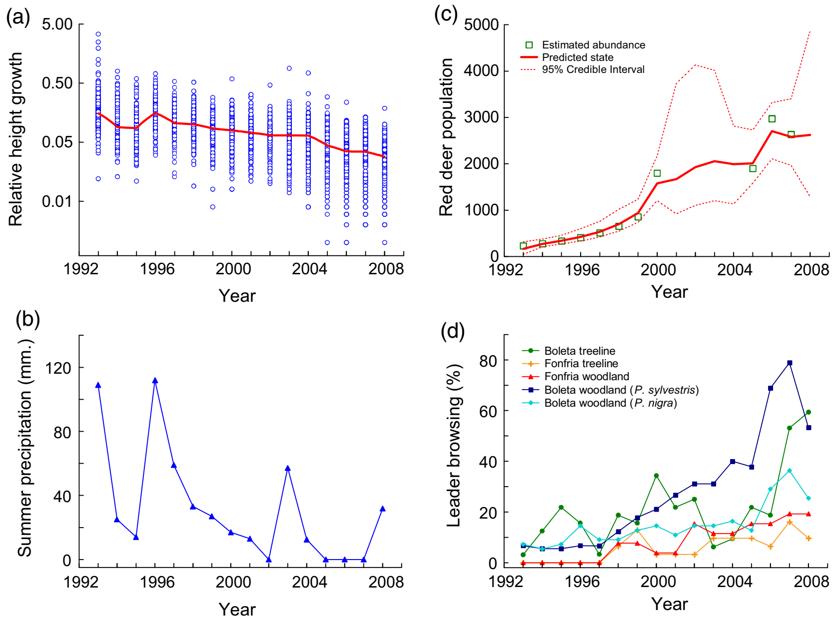

Fig. 2. Time series of relative height growth (RHG), precipitation variability, red deer population size and herbivory intensity in the study area from 1992 to 2008. (a) Value of RHG for each individual pine sapling and year, pooled across the four plots and two species (*Pinus sylvestris* and *P. nigra*). The thick red line is a locally weighted least-squares function fitted to enhance the local dynamics. (b) Time series of precipitation during summer (months of June, July and August). (c) Estimations of red deer abundance across the landscape based on observed yearly abundance (counts) are shown as open green squares; the latent (unobserved) states estimated with the Gompertz state-space model are shown as a solid red line, with 95% credible intervals depicted as dotted red lines. (d) Recorded proportion of saplings with the leader shoot browsed for each plot and species during the study period (1993–2008).

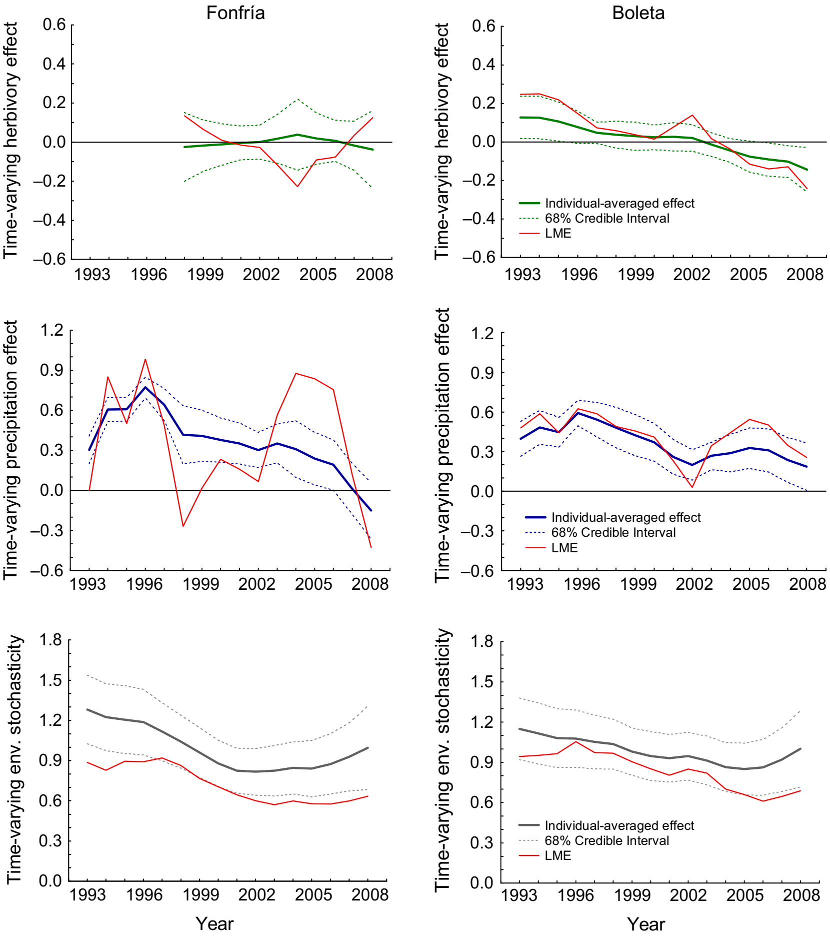

Fig. 3. Plots of time-varying coefficients measuring the effect of herbivory intensity, precipitation variability and environmental stochasticity on residual relative height growth of *Pinus sylvestris* in the treelines of Boleta and Fonfría. The effects shown are the individual-averaged time-varying impact of herbivory, summer precipitation and environmental stochasticity. For each graph, the dotted lines represent the 68% credible interval, equivalent to 1 standard deviation, while the thick red lines represent the fitting of a linear mixed-effects (LME) model to the data.

the effects of precipitation were clearly stronger during the whole time period in both plots, particularly during the first part of the series. The effects of environmental stochasticity decreased during the study period, but slightly increased at the end of the time series. The time-varying estimates from the LME model were rather similar (Fig. 3), but clearly underestimated the impact of environmental stochasticity throughout the series. Moreover, both in the treeline and in the woodland, the time-varying LME model tended to overestimate the effect of herbivory relative to the time-varying IBM (Table 1).

Figure 4 shows the time-varying effects of herbivory and precipitation on rRHG in the woodland areas obtained with the IBM, averaged over individuals. In this case, after a short transient period, the effect of herbivory was clearly stronger for *P. sylvestris* throughout the time series relative to the effects in the treelines. The magnitude of the effects of herbivory also increased at the end of the time series. However, for *P. nigra*, the herbivory effects were negligible. As in the treelines, the impact of precipitation in the woodlands was stronger during the first part of the time series. But the effect of precipitation at the woodland areas was generally lower relative to the treelines, particularly in Boleta (Fig. 4, Table 1). Regarding the relative importance of precipitation and herbivory effects, although the effect of precipitation was stronger for *P. nigra* and for *P. sylvestris* in Fonfría, the effect of herbivory was somewhat greater for *P. sylvestris* in Boleta for the whole study period (Table 1). With respect to environmental stochasticity, the individual-averaged effect displayed the same nonlinear pattern relative to the treeline areas and also tended to be underestimated by the LME model.

As suggested by the plots of the time-varying individual-level effects of herbivory and precipitation (see Figs S1 and S2), the impact of herbivory showed greater variability at the individual level than the effect of precipitation, as individual pines showed effects of the same sign more consistently in the case of precipitation effects than in the case of herbivory effects.

MODEL VALIDATION AND POSTERIOR PREDICTIVE CHECKS

The diagnostic tests revealed good mixing of the MCMC chains and rejected the hypothesis of non-convergence. The posterior correlation among parameters was low in all cases ($r < 0.2$), which suggest that the models are correctly specified and that the effects are largely identifiable.

Figure 5 shows the plot of the synthetic set of 1000 posterior simulated data sets of rRHG against the observed data, averaged over replications for each value. As the posterior data sets tend to cluster closer to the Y = X line in the time-varying IBM, the bias in the posterior predictions are lower when using this model than when using the IBM with

Table 1. Long-term effects of herbivory and summer precipitation on residual relative height growth (rRHG) of *Pinus sylvestris* and *P. nigra* in four plots of Southeastern Spain during a 16-year period

			Modelled effects					
Plot	Parameters	Effects	Herbivory	Precipitation	Stochasticity	R^2	PMSE	DIC
Fonfría treeline	Constant	IBM	0.009 (0.121)	0.428 (0.108)	1.071 (0.110)	0.314	0.639	1209.0
		LME	0.001 (0.120)	0.419 (0.101)	0.768 (0.055)	0.242	0.712	1097.0
	Time varying	IBM	−0.002 (0.046)	0.383 (0.079)	1.056 (0.152)	0.674	0.305	955.4
		LME	−0.013 (0.114)	0.383 (0.192)	0.581 (0.048)	0.476	0.494	**934.7**
Boleta treeline	Constant	IBM	−0.025 (0.034)	0.348 (0.054)	1.156 (0.105)	0.252	0.701	1529.0
		LME	−0.024 (0.031)	0.340 (0.046)	0.889 (0.056)	0.121	0.825	1425.0
	Time varying	IBM	0.010 (0.037)	0.388 (0.077)	1.049 (0.146)	0.684	0.295	**1163.0**
		LME	0.041 (0.080)	0.451 (0.192)	0.773 (0.053)	0.296	0.659	1299.0
Fonfría woodland	Constant	IBM	−0.244 (0.203)	0.322 (0.150)	1.110 (0.101)	0.278	0.678	1469.0
		LME	−0.205 (0.194)	0.246 (0.159)	0.854 (0.056)	0.158	0.789	1360.0
	Time varying	IBM	−0.198 (0.130)	0.329 (0.104)	1.058 (0.145)	0.639	0.339	**1094.0**
		LME	−0.237 (0.207)	0.333 (0.194)	0.781 (0.060)	0.280	0.677	1203.0
Boleta woodland (*P. sylvestris*)	Constant	IBM	−0.173 (0.044)	0.263 (0.044)	1.236 (0.063)	0.182	0.767	4463.0
		LME	−0.172 (0.040)	0.265 (0.039)	0.904 (0.034)	0.099	0.844	4032.0
	Time varying	IBM	−0.186 (0.060)	0.146 (0.052)	1.081 (0.087)	0.662	0.317	**3249.0**
		LME	−0.211 (0.115)	0.091 (0.132)	0.790 (0.034)	0.248	0.706	3383.0
Boleta Woodland (*P. nigra*)	Constant	IBM	0.012 (0.036)	0.232 (0.040)	1.232 (0.082)	0.188	0.761	2709.0
		LME	0.012 (0.030)	0.228 (0.035)	0.954 (0.047)	0.052	0.888	2511.0
	Time varying	IBM	0.001 (0.053)	0.209 (0.050)	1.115 (0.107)	0.630	0.347	**2003.0**
		LME	0.050 (0.097)	0.221 (0.080)	0.953 (0.054)	0.109	0.836	2341.0

The standardized modelled effects (mean ± 1 SD) are posterior averaged effects (over time and individuals) for the time-varying individual-based model (IBM), time-averaged estimates for the time-varying linear mixed-effects model (LME) and point parameter estimates for the constant parameter models (for both the IBM, averaged over individuals, and LME model). R^2 shows the proportion of variance in rRHG explained by each model, while PMSE is the predicted mean squared error of the difference between the observed data and the average value of 1000 posterior simulated stochastic data sets. The DIC is the deviance information criterion; the model minimizing this quantity provides the most parsimonious fit to the data and is shown in bold type.

constant parameters. The fitting of the LME models were particularly poor relative to the fitting of the IBM, irrespective of the type of parameters. In particular, there is much more variability in the predicted data sets of the LME model, and this approach is particularly bad when estimating extreme values (Fig. 5). The PMSE is therefore consistently larger in the LME model, in particular for the constant parameter model (Table 1).

The values for the amount of explained variance (R^2) are consistently larger for the time-varying IBM in all cases, probably due to its greater complexity. However, the DIC clearly selected the time-varying IBM as the most parsimonious models in all cases except in Fonfría treeline. In this case, the time-varying LME model appeared to provide a better fit in terms of a trade-off between model complexity and goodness-of-fit. However, as shown by the large PMSE value of this model (Table 1), there are clear signs of overfitting in this plot. This pattern is common to other plots as well: while the individual- and time-averaged estimates of environmental stochastic impacts are consistently lower for the LME model relative to the IBM, the R^2 is consistently lower and the PMSE consistently higher for both the time-varying and constant LME approaches. This is suggestive of model overfitting in the LME approach.

Discussion

Our results showed significant negative effects of herbivory and positive effects of precipitation in pine sapling height growth at the southernmost distribution limit of *P. sylvestris* and *P. nigra* during a 16-year period. However, the LME model, which neglects individual variability, tended to jointly overestimate the impact of herbivory and underestimate the effects of environmental stochasticity on plant growth relative to the IBM approach. Thus, the potential for herbivory to constrain climate-driven vegetation shifts could be lower than expected based on previous studies using aggregated individual-level data (Speed *et al.* 2011a,b; Fisichelli, Frelich & Reich 2012). This aggregation could also lead to a dismissal of the importance of other factors influencing tree growth, such as competition or soil nutrient availability. Moreover, our time-varying IBM approach showed great variability across individuals for the impact of climate and herbivory on height growth. Different responses of individuals within a population to environmental factors could have important implications for the long-term persistence of species, especially at the southernmost distribution limits, where species face adverse environmental conditions (Parmesan & Yohe 2003; Peñuelas *et al.* 2007). Greater individual variability in environmental responses increases the probability of performance success for a percentage of the population, in our study case, high height growth rates and subsequent earlier onset of reproduction (Zamora *et al.* 2001), boosting the chances for the future persistence of the population. Therefore, the use of disaggregated individual-level data and time-varying effects could help to improve the accuracy of predictions of climate-induced vegetation shifts and to

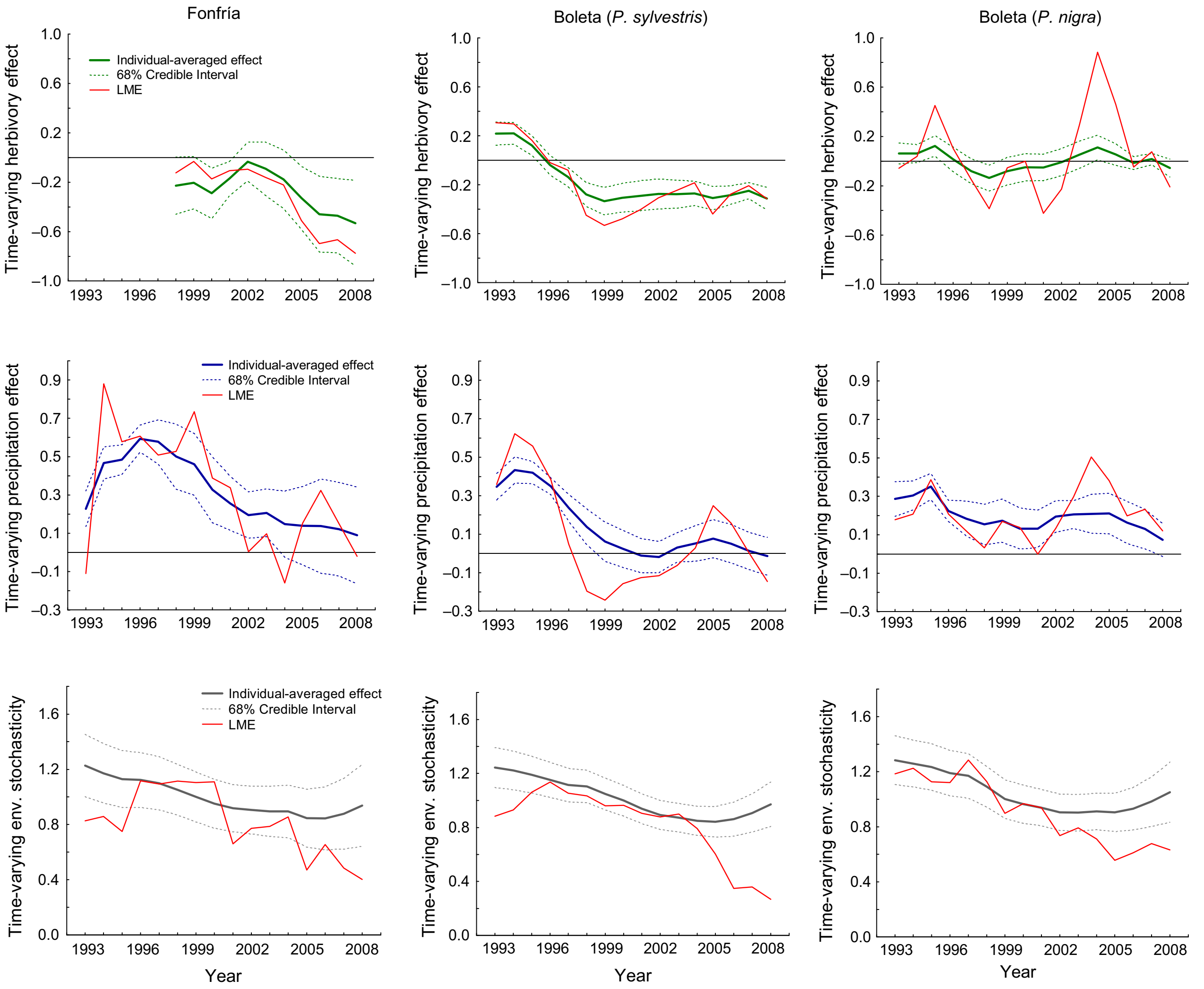

Fig. 4. Plots of time-varying coefficients measuring the effect of herbivory intensity, precipitation variability and environmental stochasticity on residual relative height growth of *Pinus sylvestris* in the woodlands of Fonfría and Boleta and *P. nigra* in Boleta woodland. The effects shown are the individual-averaged time-varying impact of herbivory, precipitation and environmental stochasticity. For each graph, the dotted lines represent the 68% credible interval, equivalent to 1 standard deviation, while the thick red lines represent the fitting of a linear mixed-effects model (LME) to the data.

disentangle the factors affecting tree growth. For the rest of the discussion, we will focus on time-varying individual-level effects.

Our hierarchical approach allowed the simultaneous modelling of the population dynamics of red deer, the dynamics of herbivory intensity and the time-varying effects of herbivory and precipitation on pine saplings height growth. Red deer abundance was driven mainly by environmental stochastic effects, increasing in a density-independent fashion throughout the landscape. The absence of predators, prevalence of mild winters, disproportionate hunting of males and difficulties of adequately implementing management policies appear to be the main reasons behind the observed rise in the red deer population (Granados *et al.* 2001; Côte *et al.* 2004; Consejería de medioambiente (CMA) 2009). At the same time, red deer population density drives herbivory intensity mainly in woodland areas, where browsing damages and the negative impact of herbivory were higher. At treelines, the impact of red deer density on herbivory intensity was lower, as red deer do not browse as frequently and intensely at the treelines than at the woodlands. However, a continued increase of the red deer population would raise the herbivory intensity at the treeline, as browsing damages increased during the last years of the study even in the treeline. Under the actual climate change scenario, an increase of herbivory pressure seems plausible as mild winters increase deer body mass (Mysterud *et al.* 2001) and winter survival (Loison, Langvatn & Solberg 1999). Furthermore, red deer could increase its foraging activity at high elevations due to predicted warming and increasing aridity in Mediterranean basin (IPCC 2013), which may decrease forest cover and food resources (key factors for deer habitat selection; Jedrzejewska *et al.* 1994; Borkowski & Ukalska 2008) at lower elevations.

Modelled effects of precipitation generally dominate over herbivory effects across plots. It is important to note that we assess the impact of herbivory on annual height growth rates

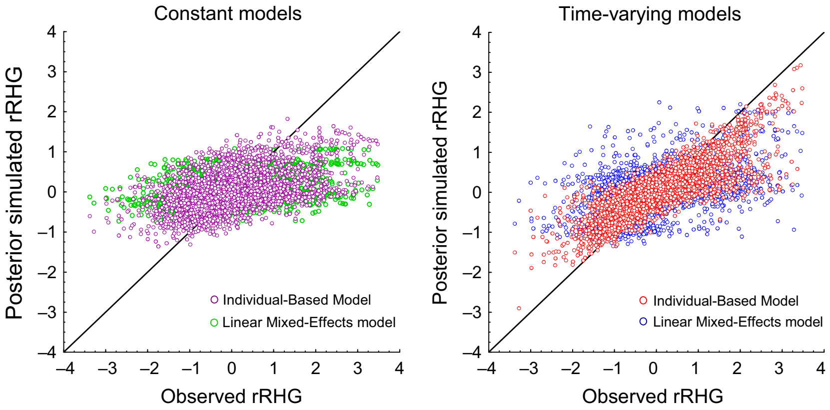

Fig. 5. Posterior simulated (predicted) data sets of residual relative height growth (rRHG) obtained with the constant and time-varying parameters models for both the individual-based model (IBM, purple and red open circles for the constant and time-varying model, respectively) and the linear mixed-effects model (LME, green and blue open circles, for the constant and time-varying model, respectively). These values were plotted against the observed rRHG, pooled for the four plots and the two species (*Pinus sylvestris* and *P. nigra*). Each dot represents the average of 1000 synthetic values randomly obtained with each fitted model (standard errors omitted for clarity). The thick black line is the Y = X regression line. Note data standardization prior to the analyses.

and that the accumulated effect of herbivory in total height growth for the study period would be probably greater than the effect on annual rates averaged over years. Nevertheless, in the plot with the highest herbivory intensity, the recorded effect of herbivory was greater than precipitation effect for the whole study period. This demonstrates the capacity of ungulate browsing to counteract the beneficial effect of climate, as has been previously observed in other ecosystems different from Mediterranean ones (e.g. Speed *et al.* 2011a; Fisichelli, Frelich & Reich 2012).

Interestingly, the relative impact of herbivory and precipitation displayed a clear variability across time. The decrease in the effects of precipitation during the later years of the series suggests a greater capacity to access water in deeper soil horizons with increasing sapling size. In contrast, the increase of herbivory effects seems mediated by the rise of the ungulate population and subsequent increase in herbivory intensity, although the browsing likelihood for a tree sapling decreased with height as saplings grow (Zamora *et al.* 2001; Speed *et al.* 2011b). In this context, the time-varying approach, which explicitly consider temporal variability in the modelled effects, greatly improves the assessment of the effects of precipitation and herbivory on plant growth accounting for the ontogenetic process of juvenile maturation and deer population dynamics. Due to the growing interest in climate-induced vegetation shifts, long-term studies analysing tree sapling growth prior to their inclusion in the overstorey layer are increasingly necessary, which need to include the temporal variability of the environmental variables affecting tree growth.

The effects of environmental stochasticity tended to decrease with time and consequently with increasing age of saplings, representing a lowered dependence of environmental conditions (Quero *et al.* 2008; Quero, Herrero & Zamora 2011) probably mediated through a better developed root system. The slight increase in stochastic effects recorded at the end of the study period could be associated to the joint effects of higher browsing damages and lowered precipitation during these years (e.g. 2005 extreme drought; Herrero & Zamora 2014). Across plots, an average of 35% of the variance in rRHG could not be explained by the fitted time-varying IBM. Competition exerts a major influence on plant performance in forest ecosystems (Clark *et al.* 2011b; Gómez-Aparicio *et al.* 2011), and this could overwhelm the impact of climate. Thus, future studies assessing environmental impacts on plant performance should account for the effects of additional factors, such as competition, to improve the estimation of growth responses under global warming scenarios.

At the treeline, the effect of precipitation on plant performance was much higher than at woodland. This suggests that the treelines are responsive zones to climatic conditions, in agreement with previous studies (e.g. Harsch *et al.* 2009; Speed *et al.* 2011a,b). The increasing warmer conditions in the study area (Herrero, Rigling & Zamora 2013; Matías & Jump 2015) could allow for the positive influence of precipitation in this harsh environment. Thus, strong effects of precipitation and weak influence of herbivory could allow tree upward expansion, although increasing browsing damages associated with increments in ungulate population and/or climatic change might limit positive climatic responses of pine saplings in the near future.

The effects of herbivory presented larger variability among individuals than the effects of precipitation, as individual pines showed effects of the same sign more consistently for precipitation. The overall stronger impact of precipitation and its lower variability between individuals suggest a more pervasive effect of precipitation at the population level, as all saplings are subjected to similar water availability. In contrast, the greater interindividual heterogeneity in the effects of herbivory is consistent with the different levels of browsing damage between individuals, in agreement with the hierarchical foraging of mammal herbivores, which includes the individual scale (Danell & Bergström 2002). In fact, while some individuals escaped ungulate herbivory by reaching browsing-free height or by the protection of spiny and/or unpalatable shrubs (e.g.

Berberis sp. or *Juniperus* sp.), others remained under the browsing threshold or lacked the protection of shrubs, thus suffering heavy damage. In this context, herbivory can act as a spatially aggregating force, creating regeneration hotspots associated with low herbivory, and patches of blocked or slowed-down regeneration associated with high herbivory.

These patterns of environmental impacts could result in heterogeneous vegetation structure in ecotones when herbivores exert a negative effect on plant growth, adding a new dimension to the predictions on climate-driven vegetations shifts based on previous works (Speed *et al.* 2011a,b; Fisichelli, Frelich & Reich 2012). At treeline areas, treeline ascension would be partially allowed through scattered individuals escaping browsing. At temperate-boreal transition zones, individual-level differences in herbivory effects would lead to complex patterns of growth between saplings of different species at small spatial scales, promoting the dominance towards boreal or temperate species depending on the ecological context and individual responses. Therefore, growth responses at individual level can modulate the 'cooling' effect of the herbivory (*sensu* Fisichelli, Frelich & Reich 2012).

Overall, our study highlights the benefits achieved by modelling ecological processes at the individual level and allowing for time-varying effects. Precipitation fluctuations showed a more pervasive and spatially homogenous effect than did herbivory on long-term height growth rate. By contrast, herbivory exerted a more spatially heterogeneous effect through individual-level damage, producing a negative impact on plant growth that can constrain treeline shifts when herbivore density is high (Speed *et al.* 2011a,b; Van Bogaert *et al.* 2011). Our results serve to delineate a prediction framework for treeline shifts under a global warming scenario, based on the relative effects of climate and herbivory. On one hand, where climate is the dominant environmental factor (and herbivory pressure is low), the treeline would gradually shift upwards through a spatially homogeneous altitudinal ascension of saplings. On the other hand, where the effect of herbivory is more important than climate, herbivory would constrain the growth of saplings, precluding the upward shift of treeline in many areas, except in patches with low herbivory, resulting in a spatially heterogeneous vegetation structure. Further studies are necessary to test these predictions, considering individual-level and temporal heterogeneity in environmental responses and treeline dynamics. Finally, modelling approaches considering individual variability would be particularly useful to assess the importance of other biotic interactions, such as host–parasite relations (e.g. mistletoe) or insect herbivory (e.g. pine processionary caterpillar), on tree species performance. Enhancing our knowledge about the relative importance of biotic interactions on plant performance and the spatial scale at which interactions exert influence would improve the forecasting of climate-driven vegetation shifts under the global warming scenario.

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Data accessibility

The data used in the manuscript are publicly available at Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.kf575 (Herrero *et al.* 2016).

References

Archibold, O.W. (1994) *Ecology of World Vegetation*. Chapman and Hall, London, UK.

Barbéro, M., Loisel, R., Quézel, P., Richardson, D.M. & Romane, F. (1998) Pines in Mediterranean basin. *Ecology and Biogeography of Pinus* (ed. D.M. Richardson), pp. 153–170. Cambridge University Press, Cambridge, UK.

Borkowski, J. & Ukalska, J. (2008) Winter habitat use by red and roe deer in pine-dominated forest. *Forest Ecology and Management*, **255**, 468–475.

Boulant, N., Kunstler, G., Rambal, S. & Lepart, J. (2008) Seed supply, drought, and grazing determine spatio-temporal patterns of recruitment for native and introduced invasive pines in grasslands. *Diversity and Distributions*, **14**, 862–874.

Cairns, D.M. & Moen, J. (2004) Herbivory influences tree lines. *Journal of Ecology*, **92**, 1019–1024.

Carrer, M. (2011) Individualistic and time-varying tree-ring growth to climate sensitivity. *PLoS ONE*, **6**, e22813.

Clark, J.S. (2010) Individuals and the variation needed for high species diversity in forest trees. *Science*, **327**, 1129–1132.

Clark, J.S., Dietze, M., Chakraborty, S., Agarwal, P.K., Ibañez, I., LaDeau, S. & Wolosin, S. (2007) Resolving the biodiversity paradox. *Ecology Letters*, **10**, 647–659.

Clark, J.S., Bell, D., Chu, C.J., Courbaud, B., Dietze, M., Hersh, M. *et al.* (2010) High-dimensional coexistence based on individual variation: a synthesis of evidence. *Ecological Monographs*, **80**, 569–608.

Clark, J.S., Bell, D.M., Hersh, M.H., Kwit, M.C., Moran, E., Salk, C., Stine, A., Valle, D. & Zhu, K. (2011a) Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecology Letters*, **14**, 1273–1287.

Clark, J.S., Bell, D.M., Hersh, M.H. & Nichols, L. (2011b) Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology*, **17**, 1834–1849.

Clark, J.S., Bell, D.M., Kwit, M., Stine, A., Vierra, B. & Zhu, K. (2012) Individual-scale inference to anticipate climate-change vulnerability of biodiversity. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **367**, 236–246.

Consejería de medioambiente (CMA) (2009) *Síntesis de la evolución de las especies cinegéticas de caza mayor en Andalucía*. Egmasa, Junta de Andalucía, Spain.

Côte, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Waller, D.M. (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics*, **35**, 113–147.

Cressie, N., Calder, C.A., Clark, J.S., Hoef, J.M.V. & Wikle, C.K. (2009) Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecological Applications*, **19**, 553–570.

Danell, K. & Bergström, R. (2002) Mammalian herbivory in terrestrial environments. *Plant-Amimal Interactions: An Evolutionary Approach* (eds M. Herrera & O. Pellmyr), pp. 107–132. Blackwell, New York, NY, USA.

Daniels, M.J. (2006) Estimating red deer *Cervus elaphus* populations: an analysis of variation and cost-effectiveness of counting methods. *Mammal Review*, **36**, 235–247.

Davidson, D.W. (1993) The effects of herbivory and granivory on terrestrial plant succession. *Oikos*, **68**, 23–35.

Debain, S., Chadoeuf, J., Curt, T., Kunstler, G. & Lepart, J. (2007) Comparing effective dispersal in expanding population of *Pinus sylvestris* and *Pinus nigra* in calcareous grassland. *Canadian Journal of Forest Research*, **37**, 705–718.

Dennis, B. & Taper, M.L. (1994) Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs*, **64**, 205–224.

Dobbertin, M., Eilmann, B., Bleuler, P., Giuggiola, A., Pannatier, E.G., Landolt, W., Schleppi, P. & Rigling, A. (2010) Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed *Pinus sylvestris* forest. *Tree Physiology*, **30**, 346–360.

Edenius, L., Danell, K. & Nyquist, H. (1995) Effects of simulated moose browsing on growth, mortality, and fecundity in scots pine: relations to plant productivity. *Canadian Journal of Forest Research*, **25**, 529–535.

Engen, S., Bakke, Ø. & Islam, A. (1998) Demographic and environmental stochasticity — concepts and definitions. *Biometrics*, **54**, 840–846.

Fisichelli, N., Frelich, L.E. & Reich, P.B. (2012) Sapling growth responses to warmer temperatures 'cooled' by browse pressure. *Global Change Biology*, **18**, 3455–3463.

Gelman, A. (2006) Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis*, **1**, 515–533.

Gelman, A., Park, D.K., Ansolabehere, S., Price, P.N. & Minnite, L.C. (2001) Models, assumptions and model checking in ecological regressions. *Journal of the Royal Statistical Society: Series A*, **164**, 101–118.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004) *Bayesian Data Analysis*. Chapman and Hall/CRC, Boca Raton, FL, USA.

Gómez-Aparicio, L., García-Valdes, R., Ruiz-Benito, P. & Zavala, M.A. (2011) Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. *Global Change Biology*, **17**, 2400–2414.

Granados, J.E., Cabrera, M.C., García, J. & Fandos, P. (2001) El Ciervo Común (*Cervus elaphus* Linneo, 1758) en el Parque Natural de la Sierra de Baza (Granada). *Galemys*, **13**, 27–37.

Hammond, J.L. (1973) Two sources of error in ecological correlations. *American Sociological Review*, **38**, 764–777.

Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.

Herrero, A., Rigling, A. & Zamora, R. (2013) Varying climate sensitivity at the dry distribution edge of *Pinus sylvestris* and *P. nigra*. *Forest Ecology and Management*, **308**, 50–61.

Herrero, A. & Zamora, R. (2014) Plant responses to extreme climatic events: a field test of resilience capacity at the southern range edge. *PLoS ONE*, **9**, e87842.

Herrero, A., Zamora, R., Castro, J. & Hódar, J.A. (2012) Limits of pine forest distribution at the treeline: herbivory matters. *Plant Ecology*, **213**, 459–469.

Herrero, A., Almaraz, P., Zamora, R., Castro, J. & Hódar, J.A. (2016) Data from: From the individual to the landscape and back: Time-varying effects of climate and herbivory on tree sapling growth at distribution limits. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.kf575.

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Isik, K. (1990) Seasonal course of height and needle growth in *Pinus nigra* grown in summer-dry Central Anatolia. *Forest Ecology and Management*, **35**, 261–270.

Jedrzejewska, B., Okarma, H., Jedrzejewski, W. & Milkowski, L. (1994) Effects of exploitation and protection on forest structure, ungulate density and wolf predation in Bialowieza primeval forest, Poland. *Journal of Applied Ecology*, **31**, 664–676.

Kaarlejärvi, E., Hoset, K.S. & Olofsson, J. (2015) Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. *Global Change Biology*, **21**, 3379–3388.

Laake, J.L., Buckland, S.T., Anderson, D.R. & Burnham, K.P. (1993) *Distance User's Guide*. Colorado State University, Fort Collins, Colorado, CO, USA.

Link, W.A. & Eaton, M.J. (2012) On thinning of chains in MCMC. *Methods in Ecology and Evolution*, **3**, 112–115.

Loison, A., Langvatn, R. & Solberg, E.J. (1999) Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography*, **22**, 20–30.

Martínez-Vilalta, J., López, B., Loepfe, L. & Lloret, F. (2012) Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia*, **168**, 877–888.

Matías, L. & Jump, A.S. (2012) Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: the case of *Pinus sylvestris*. *Forest Ecology and Management*, **282**, 10–22.

Matías, L. & Jump, A.S. (2015) Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shifts of two woody species. *Global Change Biology*, **21**, 882–896.

Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R. & Steinheim, G. (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature*, **410**, 1096–1099.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T. & Suominen, O. (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, **15**, 2681–2693.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Peñuelas, J., Ogaya, R., Boada, M. & Jump, A.S. (2007) Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography*, **30**, 829–837.

Post, E. & Pedersen, C. (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 12353–12358.

Quero, J.L., Herrero, A. & Zamora, R. (2011) Linking stochasticity to determinism of woody plant recruitment in a mosaic landscape: a spatially explicit approach. *Basic and Applied Ecology*, **12**, 161–171.

Quero, J.L., Gomez-Aparicio, L., Zamora, R. & Maestre, F.T. (2008) Shifts in the regeneration niche of an endangered tree (*Acer opalus* ssp. *granatense*) during ontogeny: using an ecological concept for application. *Basic and Applied Ecology*, **9**, 635–644.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, W.S. (1950) Ecological correlations and the behavior of individuals. *American Sociological Review*, **15**, 351–357.

Sanz-Elorza, M., Dana, E.D., Gonzalez, A. & Sobrino, E. (2003) Changes in the high-mountain vegetation of the central Iberian peninsula as a probable sign of global warming. *Annals of Botany*, **92**, 273–280.

Schuessler, A.A. (1999) Ecological inference. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 10578–10581.

Speed, J.D.M., Austrheim, G., Hester, A.J. & Mysterud, A. (2010) Experimental evidence for herbivore limitation of the treeline. *Ecology*, **91**, 3414–3420.

Speed, J.D.M., Austrheim, G., Hester, A.J. & Mysterud, A. (2011a) Browsing interacts with climate to determine tree-ring increment. *Functional Ecology*, **25**, 1018–1023.

Speed, J.D.M., Austrheim, G., Hester, A.J. & Mysterud, A. (2011b) Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *Forest Ecology and Management*, **261**, 1344–1352.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Linde, A. (2014) The deviance information criterion: 12 years on. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **76**, 485–493.

Van Bogaert, R., Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M. & Callaghan, T.V. (2011) A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography*, **38**, 907–921.

Zamora, R., Gomez, J.M., Hodar, J.A., Castro, J. & Garcia, D. (2001) Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. *Forest Ecology and Management*, **144**, 33–42.

Zeng, Z., Nowierski, R.M., Taper, M.L., Dennis, B. & Kemp, W.P. (1998) Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. *Ecology*, **79**, 2193–2209.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Plots of time-varying coefficients measuring the individual-level effects of herbivory intensity and precipitation variability on residual Relative Height Growth in the treeline areas.

Figure S2. Plots of time-varying coefficients measuring the individual-level effects of herbivory intensity and precipitation variability on residual Relative Height Growth in the woodland areas.

Table S1. Modelled effects of the long-term impacts of red deer population density, summer precipitation and environmental stochasticity on herbivory intensity.

Appendix S1. BUGS code for the fitting of the time-varying Individual-Based Model.

Appendix S2. BUGS code for the fitting of the time-varying Linear Mixed-Effect Model.

Appendix S3. BUGS code for the fitting of the Individual-Based Model with constant parameters.

Appendix S4. BUGS code for the fitting of the Linear Mixed-Effect Model with constant parameters.