

1       **From the individual to the landscape and back: Time-varying**  
2                   **effects of climate and herbivory on tree sapling growth at**  
3                                   **distribution limits**

4  
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17       Running headline: Time-varying effects on growth at individual level

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## 21 **Summary**

- 22 1. As herbivory can modulate climate-induced shifts in species distribution,  
23 disentangling the relative importance of herbivory and climate on plant growth can  
24 help to predict and manage future changes in vegetation, such as those occurring at  
25 treeline areas.
- 26 2. An individual-based hierarchical Bayesian time-series model (Individual-Based  
27 Model; IBM) was developed to estimate the time-varying impact of climate and  
28 herbivory on individual pine-sapling height growth in woodland and treeline  
29 ecosystems of Southern Europe during a 16-year period. The performance of the  
30 IBM was compared to a Linear Mixed-Effects (LME) model to test for potential  
31 inferential effects when individual variability is marginalized. Time-varying models  
32 were also compared to constant parameter approaches.
- 33 3. Model fitting and posterior predictive checking suggests a better statistical  
34 performance of individual-scale, time-varying inference. LME modeling  
35 overestimated herbivory effects and underestimated environmental stochastic  
36 effects, and model validation indeed suggested severe overfitting in the LME model  
37 relative to the IBM strategy. These results reveal a potential failure of common  
38 aggregation strategies to correctly resolve the effects of climate and herbivory  
39 variability at the individual scale. Moreover, ignoring the time-varying nature of the  
40 effects may preclude the correct estimation of the temporal scale of climate and  
41 herbivory impacts.
- 42 4. In general, we found stronger individual- and time-averaged effects of summer  
43 precipitation relative to the effects of herbivory, particularly at the treelines. Also,  
44 individual pines responses showed effects of the same sign more consistently in the  
45 case of precipitation. This suggests that precipitation is more pervasive at the

46 population level, while herbivory act as a spatially aggregating force through  
47 individual-level damage.

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

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

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## 65 **Introduction**

66 Climate and herbivory, as bottom-up and top-down forces, respectively, are among the  
67 main factors influencing the distribution, performance, and abundance of plant species  
68 (Davidson 1993; Archibold 1994; Speed *et al.* 2010). Under the current climate change  
69 scenario, fast distributional shifts of species are expected in response to increasing warmer  
70 conditions (Parmesan & Yohe 2003; Harsch *et al.* 2009; Matías & Jump 2015). Herbivory

71 can modulate such changes, inhibiting or exacerbating plant responses to climate. Lower  
72 herbivory pressure could favor upward expansions of woody plant species associated with  
73 climate (Sanz-Elorza *et al.* 2003; Cairns & Moen 2004). However, the role of herbivores in  
74 changing tree and shrub distributions generally opposes that of climate warming; whereas  
75 warmer temperatures facilitate the spread of trees and shrubs to higher latitudes and  
76 altitudes, high densities of herbivores can constrain upward and northward movements  
77 (Post & Pedersen 2008; Olofsson *et al.* 2009; Speed *et al.* 2010; Kaarlejärvi, Hoset &  
78 Olofsson 2015). Changes in herbivore density are thus likely to contribute to shifts in  
79 community composition in addition to, and possibly in interaction with, the better-studied  
80 climatic drivers. Therefore, disentangling the relative importance of climate and herbivory  
81 on plant performance can help to forecast species distributional changes and improve our  
82 understanding of the complex interplay between climate and biotic interactions. In addition,  
83 insights into the interactions between herbivores and climate, as drivers of shifts in  
84 community composition, have the potential for facilitating the management of herbivore  
85 populations to buffer the effect of global warming on distribution shifts in alpine plant  
86 communities.

87         Traditionally, the effects of climate and herbivory have been analyzed at the  
88 population or landscape level through the aggregation of individual-level data. However,  
89 aggregation over the individual scale to higher scales can degrade information and hide  
90 individual characteristics not apparent from group-level attributes (Clark 2010; Clark *et al.*  
91 2011a). Recent studies using disaggregated individual data have shown the importance of  
92 individual-level variation. In fact, this variation allows species to differ in their distributions  
93 of responses to the environment, although populations might not differ on average, playing  
94 an important role in species coexistence in forest ecosystems (Clark *et al.* 2007; Clark  
95 2010). The individual scale has also been considered in studies assessing vulnerability of

96 tree species to climate change, demonstrating its importance in plant performance (Clark *et*  
97 *al.* 2012). These approaches can be framed within the ecological (or aggregate) inference  
98 problem, which aims at drawing conclusions about individual-level behavior from  
99 aggregate-level data (Schuessler 1999). It is well known that the marginalization of  
100 individual-level data on statistical summaries or aggregates degrades statistical inference by  
101 biasing the estimates of ecological regression parameters to the group average (see  
102 Robinson 1950; Hammond 1973; Gelman *et al.* 2001). Thus, the analysis of climate and  
103 herbivory impact at the individual level could provide new insights into the understanding  
104 of the interplay between climate and biotic interactions.

105         The goal of the present study is to analyze tree-sapling height-growth response to  
106 climate and herbivory in Mediterranean pinewoods at the individual and population levels.  
107 Height growth is related to reproductive age in pine saplings, which represent the near  
108 future of the forest (Zamora *et al.* 2001; Herrero *et al.* 2012). This is especially relevant at  
109 species distribution leading edge such treelines, where climate-driven range expansions can  
110 occur and populations are composed mainly of young individuals (Matías & Jump 2012;  
111 2015). The study was performed at the southernmost distribution limit of two widespread  
112 species (*Pinus sylvestris* L. and *P. nigra* Arnold), considering woodland as well as treeline  
113 areas in order to test whether pine saplings respond differently to climate and herbivory at  
114 their altitudinal margin and to detect the potential for upward migration. Both climate and  
115 herbivory can severely constrain height growth in Mediterranean areas, especially at  
116 species southern distribution limits (Hampe & Petit 2005; Herrero *et al.* 2012), hampering  
117 upward migrations at the treeline. Thus, disentangling the relative effects of climate and  
118 herbivory in height growth can help to detect species range shifts and to assess future  
119 viability of tree populations under the current climate change scenario.

120           Climate fluctuations, saplings height growth, herbivory damage, and the number of  
121 ungulates were monitored for 16 years. This period of time is sufficient to properly analyze  
122 demographic dynamics of a sapling cohort, as both *P. sylvestris* and *P nigra* are able to  
123 reach maturity in 12-15 years (Debain *et al.* 2007; Boulant *et al.* 2008). Thus, plant  
124 performance was analyzed over the entire lifespan of target saplings, prior to adult  
125 reproductive phase, the sapling phase being a key ontogenetic stage for forest expansion.  
126 We use an individual-based hierarchical Bayesian time-series model (hereafter Individual-  
127 Based Model; IBM) to estimate the effects of climate and herbivory on the temporal  
128 dynamics of pine-sapling height growth at the individual level. Bayesian hierarchical  
129 modeling allows the optimal structuring of different sources of uncertainty and  
130 heterogeneity arising from the process, parameters, and data levels of ecological models  
131 (Cressie *et al.* 2009). Given that we are dealing with an ontogenetic process, our IBM  
132 approach explicitly incorporate a time-varying modeling scheme for estimating the possibly  
133 shifting effects of herbivory and precipitation on tree sapling growth across time (see Carrer  
134 2011 for a similar approach). In addition, the effects of climate and herbivory on plant  
135 growth were also modeled using a standard Linear Mixed-Effects (hereafter LME) model,  
136 where individual-level data were aggregated at the population level (e.g., Speed *et al.*  
137 2011a; Martínez-Vilalta *et al.* 2012). This will allow us to test for the potential inferential  
138 effects of aggregation at the individual scale (Clark *et al.* 2011a). Finally, time-varying  
139 approaches were also compared to constant parameter approaches for both IBM and LME  
140 models to assess the influence of temporal variability in the estimated effects.

141           In summary, the aims of this study are: 1) to test for the relative importance of  
142 climate and herbivory in pine-sapling height-growth trends at the individual (IBM) and  
143 population level (LME); and 2) to compare the effect of climate and herbivory in treeline  
144 and woodland areas.

## 145 **Materials and Methods**

### 146 *Study site*

147 The study was conducted at Sierra de Baza Natural Park (SE Spain, 2°51'48''W,  
148 37°22'57''N). *P. sylvestris* and *P. nigra* populations at Sierra de Baza are among the  
149 southernmost populations of the two species (Barbéro *et al.* 1998). The climate is  
150 Mediterranean, characterized by cold winters and hot summers, with pronounced summer  
151 drought. Precipitation is concentrated mainly in autumn and spring, with an annual rainfall  
152 of  $495 \pm 33$  mm (mean  $\pm$  SE for 1991-2006 period), and summer rainfall (months of June,  
153 July and August) of  $31 \pm 9$  (mean  $\pm$  SE for 1991-2006 period; Cortijo Narváez  
154 meteorological station, 1360 m a.s.l.). The main herbivore affecting height growth of the  
155 target species is the regional red deer (*Cervus elaphus* L.), with an approximate population  
156 of 2600 individuals in 2007 ( $5.04$  ind/km<sup>2</sup>; CMA 2009).

157

### 158 *Sampling design, ungulate population, browsing damages and plant* 159 *performance*

160 This study was conducted in two native forests (1700-2100 m a.s.l.) from 1993 to 2008. In  
161 each forest, we selected two plots (approximately 1 ha each), one in the woodland and the  
162 other at the treeline. The first forest, Boleta hereafter, is a mixed forest of *P. sylvestris* and  
163 *P. nigra* growing intermingled with an understorey composed mainly of *Juniperus*  
164 *communis* L., *J. sabina* L., *Berberis hispanica* L., *Astragalus granatensis* Lange, and  
165 *Hormatophylla spinosa* (L.) P. Küpfer. *P. sylvestris* sapling density was  $142 \pm 24.3$  and  $72$   
166  $\pm 12.7$  ind/ha in woodland and treeline, respectively; and *P. nigra* density was  $88 \pm 34.3$   
167 and  $2 \pm 2$  ind/ha. Pine-sapling density was measured with 10 transects of 50 m length and  
168 10 m wide at each plot in 2008. The second forest, Fonfría hereafter, is composed  
169 exclusively of *P. sylvestris* with an understorey composed mainly by *J. communis* and *J.*

170 *sabina*. Sapling density was  $576 \pm 91.8$  and  $142 \pm 35.1$  ind/ha for woodland and treeline,  
171 respectively. Overall, we sampled 234 pine saplings of *P. sylvestris* and *P. nigra*: 90 *P.*  
172 *sylvestris* and 55 *P. nigra* in Boleta woodland, 32 *P. sylvestris* in Boleta treeline, 31 *P.*  
173 *sylvestris* in Fonfría woodland, and 26 *P. sylvestris* in Fonfría treeline. Monitored  
174 individuals were established non-reproductive saplings (older than 3 years old) at the  
175 beginning of the study.

176 We use red deer density data from 1993 to 2008. The data from 1993 to 2000 were  
177 extracted from Granados *et al.* (2001) and data from 2005 to 2007 from CMA (2009). Both  
178 studies used lineal transects and analyzed data using DISTANCE software (Laake *et al.*  
179 1993) and Fourier series to produce red deer density estimations. Data from 2001 to 2004  
180 and 2008 were estimated through a state-space model (see *Model Construction* section).

181 Height and browsing damage data for pine saplings were obtained in samplings  
182 performed in 1995, 1998, 2004, 2006 and 2008. All the measured saplings were tagged and  
183 mapped in the beginning of the study to enable individual identification over the study  
184 years. Tags were renewed when necessary to assure correct identification. Age was  
185 estimated as number of whorls (Edenius, Danell & Nyquist 1995) for each sapling in 1995.  
186 Beyond the measurement of height, annual internode growth (trunk elongation) and leader  
187 browsing were measured for the current year and the previous years (two previous years for  
188 the first sampling and the years needed until reach the internode measured in the previous  
189 sampling for the following samplings). Annual internode growth was measured following  
190 yearly whorls and bud scars, as both *P. sylvestris* and *P. nigra* showed one flush per year in  
191 the study area. Saplings height corresponding to previous years was estimated based on  
192 measurements of annual internode growth. Then, annual height over the period 1993-2008  
193 was used to calculate annual Relative Height Growth (hereafter RHG), defined as the ln-  
194 ratio between current year height and previous year height. Following Speed *et al.* (2011a)



195 we subtracted the biological trend due to the aging of pines with the regression model  
196  $\ln(x_{i,k,t+1}/x_{i,k,t}) = a_k + b_k \times \log_e(\text{age}_{i,k,t})$ , where  $x_{i,k,t}$  is the height of each pine  $i$  in each plot  $k$  at  
197 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  $t$ ,  
198 and  $\text{age}_{i,k,t}$  is the age of each individual pine  $i$  in each plot  $k$  and time  $t$ . Parameters  $a_k$  and  $b_k$   
199 are the regression intercept and slope, respectively, for each plot. The residuals were  
200 subtracted from this regression to obtain a standardized series of residual RHGs, hereafter  
201 rRHG. Leader browsing occurs when the terminal leader shoot of the sapling was lost to  
202 herbivory, causing a loss in the apical dominance of the pine sapling, which generally  
203 implies a reduction in height growth (as the browsed sapling need to grow in height by a  
204 lateral branch). Leader browsing of the previous years were detected by clear bifurcation or  
205 strong changes of the direction in the main stem (therefore a conservative measurement). In  
206 this context, is important to note that browsing causes more than 98 % of the losses of  
207 apical dominance in *P. sylvestris* in the study area (Zamora *et al.* 2001). Measurements  
208 were made in autumn, when annual internode growth was resumed and after the main  
209 browsing period in the study area (i.e. summer). We have not detected any sapling  
210 mortality related to herbivory during the study.

211

## 212 **Modeling individual-level responses to climate and herbivory**

### 213 *Model construction*

214 We constructed an IBM to estimate the joint time-varying effects of precipitation and  
215 herbivory on the temporal dynamics of rRHG at the individual-pine level (e.g. Clark *et al.*  
216 2010). Our approach is based on the simultaneous estimation of three linked models (see  
217 Fig. 1): a stochastic dynamics model for the red deer population at the landscape level; a  
218 model relating herbivory intensity to precipitation variability and red deer density at the

219 plot level; and a third one modeling the individual level response of rRHG to precipitation  
 220 and herbivory intensity at the plot level.

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

227

$$228 \quad n_t = n_{t-1} + r \left( 1 - \frac{n_{t-1}}{K} \right) + \varepsilon_t \quad \text{eqn. 1}$$

229

230 where  $n_t$  is the  $\log_e$ -transformed true population size at time  $t$ ,  $r$  is the intrinsic rate of  
 231 increase,  $K$  the carrying capacity at the landscape level and  $\varepsilon_t$  is the stochastic term for the  
 232 environmental and demographic process error. The term  $\varepsilon_t$  is sequentially independent and  
 233 identically distributed noise having a normal distribution with mean 0 and variance  $\Sigma_{n_t}$ ,  $\varepsilon_t \sim$   
 234  $N(0, \Sigma_{n_t})$ . The matrix  $\Sigma_{n_t}$  is decomposed into an environmental ( $\sigma_{n_t}^2$ ) and a demographic  
 235 component ( $\mathbf{D}_t$ ),  $\Sigma_{n_t} = \sigma_{n_t}^2 + \mathbf{D}_t$ , where  $\sigma_{n_t}^2$  stand for the impact of environmental noise, and  
 236  $\mathbf{D}_t$  for the impact of demographic stochasticity. The diagonal matrix  $\mathbf{D}_t = [\delta^2/\exp(n_1), \dots,$   
 237  $\delta^2/\exp(n_s)]^T$  reflects the demographic variance affecting the dynamics of the red deer from  
 238 time  $t-1$  to  $t$ , which scales inversely with population size (e.g. Engen, Bakke & Islam 1998).  
 239 Finally, the population estimates are linked to the true abundances through a Gaussian  
 240 observation model,

241

$$242 \quad y_t \sim N(n_t, \tau_{n_t}^2) \quad \text{eqn. 2}$$

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

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

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

260

$$261 \quad h_{k,t} = \eta_k + \varphi_k n_t + \zeta_k p_t + \varepsilon_{h_t,k,t} \quad \text{eqn. 3}$$

262

263 where  $\eta_k$  is the intercept,  $\varphi_k$  and  $\zeta_k$  are the effects of red deer abundance and detrended  
 264 summer precipitation on herbivory intensity ( $h_{k,t}$ ), respectively; and  $\varepsilon_{h_t,k,t}$  is sequentially  
 265 independent noise distributed according to a normal distribution with mean 0 and variance  
 266  $\sigma_{h_t}^2$ .

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

270

$$271 \quad \text{rRHG}_t = \mathbf{c}_k + \boldsymbol{\beta}_{k,t} h_{k,t} + \boldsymbol{\gamma}_{k,t} p_{t-1} + \boldsymbol{\varepsilon}_{x_{k,t}} \quad \text{eqn. 4}$$

272

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

289

$$\begin{aligned}
\beta_{k,t} &= \beta_{k,t-1} + \varepsilon_{\beta_{k,t},t} \\
\gamma_{k,t} &= \gamma_{k,t-1} + \varepsilon_{\gamma_{k,t},t} \\
\sigma_{k,t} &= \sigma_{k,t-1} + \varepsilon_{\sigma_{k,t},t}
\end{aligned}
\tag{eqn. 5}$$

291

292 where  $\varepsilon_{\beta_{k,t},t}$ ,  $\varepsilon_{\gamma_{k,t},t}$  and  $\varepsilon_{\sigma_{k,t},t}$  stand for the independent and identically distributed  
293 (random) noise on the red deer abundance, summer precipitation and environmental  
294 stochastic time-varying effects on individual pines, following normal distributions with 0  
295 means and non-zero process variances  $\rho_{\beta_{k,t},t}^2$ ,  $\rho_{\gamma_{k,t},t}^2$  and  $\rho_{\sigma_{k,t},t}^2$ .

296 We decomposed the effects of summer precipitation and red deer abundance on  
297 rRHG through both direct effects of these variables and indirect effects considering the  
298 response of leader browsing to precipitation and red deer abundance (Fig. 1). Hence, a  
299 composite parameter for the downscaled effect of red deer abundance at the landscape level  
300 on individual rRHG will be denoted by  $H_{k,i,t}$ ; this parameter is simply the product of the  
301 effect of red deer abundance (landscape level) on herbivory intensity (plot level) and the  
302 effect of herbivory intensity on individual-level rRHG:  $H_{k,i,t} = \varphi_k \times \beta_{i,k,t}$ . In the same  
303 manner, a composite parameter for the effect of summer precipitation on rRHG ( $R_{k,i,t}$ ) can  
304 be obtained by summing the direct effect of summer precipitation on rRHG and the product  
305 of the effect of summer precipitation on herbivory intensity:  $R_{k,i,t} = \gamma_k + (\zeta_k \times \beta_{i,k,t})$ . Then,  
306 we derived population-level summary statistics to describe the collective response of the  
307 rRHG of individual pines to precipitation and herbivory at each plot studied, as well as the  
308 average environmental stochasticity at the plot level (Fig. 1). In particular, for each plot we  
309 estimated the posterior averaged modeled effect across time within individuals, and an  
310 average per plot over time and individuals (e.g. Clark *et al.* 2010). Let  $\theta_t$  stand for the  
311 averaged individual-level response to a given effect (composite herbivory or summer  
312 precipitation) at time  $t$ , or the averaged individual-level impact of environmental

313 stochasticity. The time-varying posterior estimate for these parameters, calculated over  $m$   
 314 individuals, is derived for each plot  $k$  as:

$$315 \quad \boldsymbol{\theta}_{k,t} = \frac{\sum_i^m \theta_{i,k,t}}{m-1} \quad \text{eqn. 6}$$

316 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  
 317 quantity averaged over  $T$  time steps and  $m$  individuals for each plot  $k$  is obtained as:

$$319 \quad \boldsymbol{\theta}_k = \frac{\sum_1^T \sum_i^m \theta_{i,k,t}}{(m-1)(T-1)} \quad \text{eqn. 7}$$

320

321

### 322 *Prior specification, parameter estimation and model validation*

323 We fitted the IBM using Markov Chain Monte Carlo (MCMC) integration through Gibbs  
 324 sampling. To let the likelihood dominate the prior, we placed weakly informative prior  
 325 distributions on the unknown quantities. Uniform distributions were placed on the standard  
 326 deviations of the environmental and demographic noise terms in the Gompertz state-space  
 327 model, and in the terms for environmental and process parameter noise in eqns. 3-5:

328  $\sigma_{n_t}, \delta, \sigma_{h_t}, \sigma_{x_{i,t}}, \rho_{\beta_{k,t,t}}, \rho_{\gamma_{k,t,t}}, \rho_{\sigma_{k,t,t}} \sim U(0, 3)$ ; see Gelman 2006). Note that these parameters

329 are non-exchangeable between individuals. The location parameters, the constant level  
 330 terms and the initial values for the time-varying parameters were given flat prior normal

331 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  $K$

332 were truncated at a lower level of 0 to omit biologically implausible values. We

333 programmed the IBM in the BUGS language using the R package BRugs (R Development

334 Core Team 2011). We ran three independent Markov chains with dispersed initial values

335 for 23,000 iterations, and discarded the first 20,000 as a burn-in period. To increase the  
 336 precision of Bayesian estimates, we merged the unthinned chains (Link & Eaton 2012). We  
 337 used the R package BOA to derive the posterior estimates of parameters and latent states,  
 338 and to check the convergence of the chains using standard diagnostic tests (see Gelman *et*  
 339 *al.* 2004).

340 We used posterior predictive checking (Gelman *et al.* 2004) to assess the predictive  
 341 ability of the fitted IBM. This is a convenient strategy for checking model adequacy (see  
 342 also Clark *et al.* 2010). We used the fitted model to randomly derive through simulation  
 343 1000 synthetic time series of rRHG for each individual pine. We then plotted the average of  
 344 these synthetic (posterior predicted) time series against the true value used to fit the model.  
 345 The closer the synthetic datasets are to the true observations, the better the model adequacy  
 346 to the focal dataset (Gelman *et al.* 2004). We also used posterior predictive checks to  
 347 compare the IBM in eqn. 4 to the standard LME model (Speed *et al.* 2011a, Martínez-  
 348 Vilalta *et al.* 2012), in which individuals are modelled as random factors and herbivory and  
 349 climate variables are treated as fixed effects. This model, in which the growth of  
 350 individuals is an aggregate quantity (e.g., Clark 2010) can be written as:

351

$$352 \quad \text{rRHG}_t = \mathbf{c}_k + \beta_{k,t} h_{k,t} + \gamma_{k,t} p_{t-1} + \varepsilon_t \quad \text{eqn. 8}$$

353

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

356

$$357 \quad \begin{aligned} \beta_{k,t} &= \beta_{k,t-1} + \varepsilon_{\beta_{k,t}} \\ \gamma_{k,t} &= \gamma_{k,t-1} + \varepsilon_{\gamma_{k,t}} \\ \sigma_{k,t} &= \sigma_{k,t-1} + \varepsilon_{\sigma_{k,t}} \end{aligned} \quad \text{eqn. 9}$$

358 Note that in this model inter-individual variability is indeed allowed in the constant terms  
 359 (intercepts)  $c_i$ . Again, the location parameters and the constant level terms were given flat  
 360 prior normal distributions, while uniform distributions were placed on the standard  
 361 deviations of the environmental and process parameter noise (see above and see BUGS  
 362 code in Appendix S2 in Supporting Information). A critical, usually untested assumption of  
 363 this modeling scheme is that individual responses are treated as stochastic realizations of a  
 364 common underlying process, so that climate and herbivory are assumed to affect all  
 365 individuals in a similar way. To test this assumption, posterior predicted datasets for the  
 366 LME in eqn. 8 were compared directly to the predictions from the IBM in eqn 4. We also  
 367 used posterior predictive checking to compare the relative performance of the time-varying  
 368 parameter scheme to the standard constant parameter models (e.g., Speed *et al.* 2011a;  
 369 Fisichelli, Frelich & Reich 2012); in this case, the IBM with constant parameters was  
 370 specified as

371

$$372 \quad \text{rRHG}_t = \mathbf{c}_k + \beta_k h_{k,t} + \gamma_k p_{t-1} + \boldsymbol{\varepsilon}_{x_k,t} \quad \text{eqn. 10}$$

373

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

375

$$376 \quad \text{rRHG}_t = \mathbf{c}_k + \beta_k h_{k,t} + \gamma_k p_{t-1} + \boldsymbol{\varepsilon}_t$$

377  $\quad \quad \quad$  eqn. 11

378

379 Overall, we fitted 4 models (IBM or LME, constant or time-varying) for each of the 4  
 380 plots and two species (20 models). For each model, we computed the proportion of variance  
 381 in rRHG explained by each model ( $R^2$ ) and the Predicted Mean Squared Error (PMSE)  
 382 between the posterior predicted data and the true observations in both the IBM and the



383 LME model. Finally, we calculated the Deviance Information Criterion (DIC) for each  
384 model to compare their relative performance in terms of model complexity and fit  
385 (Spiegelhalter *et al.* 2014). The most parsimonious model will minimize this quantity. We  
386 compared model adequacy by jointly interpreting the values for  $R^2$ , PMSE and DIC.

387

## 388 **Results**

### 389 *Population dynamics of red deer and trends in precipitation and herbivory*

390 Figure 2c showed population dynamics of red deer during the study period. The carrying  
391 capacity of the red deer population at the landscape level (parameter  $K$  in eqn. 1) was  
392 estimated at 3093.319 individuals, and the intrinsic growth rate ( $r$ ) at  $1.125 \pm 0.516$ .  
393 According to the fitting of the state-space Gompertz population-dynamics model, 71.271%  
394 of the temporal variability in red deer abundance was driven by environmental stochastic  
395 effects, while intra-specific interactions (density dependence) accounted only for the  
396 28.684% of this variance. Finally, the relative impact of demographic stochasticity was  
397 negligible (0.045%).

398         The amount of precipitation during summer declined significantly throughout the  
399 study period (Fig. 2b;  $r = -0.55$ ,  $P_{\text{boot}} = 0.012$ , calculated using 10000 MC samples). By  
400 contrast, herbivory intensity (percentage of saplings displaying leader browsing) increased  
401 significantly over time in all plots ( $P_{\text{boot}} < 0.05$ ; Fig. 2d). There was large inter-plot  
402 variability in herbivory intensity, with very high values in Boleta woodland for *P. sylvestris*  
403 (up to 80% of browsed saplings) and relatively low values at Fonfría treeline ( $< 20\%$ ).

404

### 405 *Effects of red deer density and precipitation on herbivory intensity*

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

#### 409 *Effects of herbivory and precipitation on rRHG*

410 Figure 3 shows the time-varying effects of herbivory and precipitation on rRHG in the  
411 treelines obtained with the IBM, averaged over individuals. The effect of herbivory was  
412 negligible until the end of the time series in Boleta, but was non-significant in Fonfría  
413 throughout the time series. In contrast, the effects of precipitation were clearly stronger  
414 during the whole time period in both plots, particularly during the first part of the series.  
415 The effects of environmental stochasticity decreased during the study period, but slightly  
416 increased at the end of the time series. The time-varying estimates from the LME model  
417 were rather similar (Fig. 3), but clearly underestimated the impact of environmental  
418 stochasticity throughout the series. Moreover, both in the treeline and in the woodland the  
419 time-varying LME model tended to overestimate the effect of herbivory relative to the  
420 time-varying IBM (Table 1).

421 Figure 4 shows the time-varying effects of herbivory and precipitation on rRHG in  
422 the woodland areas obtained with the IBM, averaged over individuals. In this case, after a  
423 short transient period the effect of herbivory was clearly stronger for *P. sylvestris*  
424 throughout the time series relative to the effects in the treelines. The magnitude of the  
425 effects of herbivory also increased at the end of the time series. However, for *P. nigra*, the  
426 herbivory effects were negligible. As in the treelines, the impact of precipitation in the  
427 woodlands was stronger during the first part of the time series. But the effect of  
428 precipitation at the woodland areas was generally lower relative to the treelines, particularly  
429 in Boleta (Fig. 4, Table 1). Regarding the relative importance of precipitation and herbivory  
430 effects, although the effect of precipitation was stronger for *P. nigra* and for *P. sylvestris* in

431 Fonfría, the effect of herbivory was somewhat greater for *P. sylvestris* in Boleta for the  
432 whole study period (Table 1). With respect to environmental stochasticity, the individual-  
433 averaged effect displayed the same nonlinear pattern relative to the treeline areas, and also  
434 tended to be underestimated by the LME model.

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

440

#### 441 *Model validation and posterior predictive checks*

442 The diagnostic tests revealed good mixing of the MCMC chains and rejected the hypothesis  
443 of non-convergence. The posterior correlation among parameters was low in all cases ( $r <$   
444  $0.2$ ), which suggest that the models are correctly specified and that the effects are largely  
445 identifiable.

446 Figure 5 shows the plot of the synthetic set of 1000 posterior simulated datasets of  
447 rRHG against the observed data, averaged over replications for each value. Since the  
448 posterior datasets tend to cluster closer to the  $Y = X$  line in the time-varying IBM, the bias  
449 in the posterior predictions are lower when using this model than when using the IBM with  
450 constant parameters. The fitting of the LME models were particularly poor relative to the  
451 fitting of the IBM, irrespective of the type of parameters. In particular, there is much more  
452 variability in the predicted datasets of the LME model, and this approach is particularly bad  
453 when estimating extreme values (Fig. 5). The PMSE is therefore consistently larger in the  
454 LME model, in particular for the constant parameter model (Table 1).

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

466

## 467 **Discussion**

468 Our results showed significant negative effects of herbivory and positive effects of  
469 precipitation in pine-sapling height growth at the southernmost distribution limit of *P.*  
470 *sylvestris* and *P. nigra* during a 16-year period. However, the LME model, which neglects  
471 individual variability, tended to jointly overestimate the impact of herbivory and  
472 underestimate the effects of environmental stochasticity on plant growth relative to the IBM  
473 approach. Thus, the potential for herbivory to constrain climate-driven vegetation shifts  
474 could be lower than expected based on previous studies using aggregated individual-level  
475 data (Speed *et al.* 2011a,b; Fisichelli, Frelich & Reich 2012). This aggregation could also  
476 lead to a dismissal of the importance of other factors influencing tree growth, such as  
477 competition or soil nutrient availability. Moreover, our time-varying IBM approach showed  
478 great variability across individuals for the impact of climate and herbivory on height  
479 growth. Different responses of individuals within a population to environmental factors

480 could have important implications for the long-term persistence of species, especially at the  
481 southernmost distribution limits, where species face adverse environmental conditions  
482 (Parmesan & Yohe 2003; Peñuelas *et al.* 2007). Greater individual variability in  
483 environmental responses increases the probability of performance success for a percentage  
484 of the population, in our study case high height-growth rates and subsequent earlier onset of  
485 reproduction (Zamora *et al.* 2001), boosting the chances for the future persistence of the  
486 population. Therefore, the use of disaggregated individual-level data and time-varying  
487 effects could help to improve the accuracy of predictions of climate-induced vegetation  
488 shifts and to disentangle the factors affecting tree growth. For the rest of the discussion, we  
489 will focus on time-varying individual-level effects.

490 Our hierarchical approach allowed the simultaneous modeling of the population  
491 dynamics of red deer, the dynamics of herbivory intensity and the time-varying effects of  
492 herbivory and precipitation on pine-saplings height growth. Red deer abundance was driven  
493 mainly by environmental stochastic effects, increasing in a density-independent fashion  
494 throughout the landscape. The absence of predators, prevalence of mild winters,  
495 disproportionate hunting of males, and difficulties of adequately implementing  
496 management policies appear to be the main reasons behind the observed rise in the red deer  
497 population (Granados *et al.* 2001; Côte *et al.* 2004; CMA 2009). At the same time, red deer  
498 population density drives herbivory intensity mainly in woodland areas, where browsing  
499 damages and the negative impact of herbivory were higher. At treelines, the impact of red  
500 deer density on herbivory intensity was lower, as red deer do not browse as frequently and  
501 intensely at the treelines than at the woodlands. However, a continued increase of the red  
502 deer population would raise the herbivory intensity at the treeline, since browsing damages  
503 increased during the last years of the study even in the treeline. Under the actual climate  
504 change scenario, an increase of herbivory pressure seems plausible as mild winters increase

505 deer body mass (Mysterud *et al.* 2001) and winter survival (Loison, Langvatn & Solberg  
506 1999). Furthermore, red deer could increase its foraging activity at high elevations due to  
507 predicted warming and increasing aridity in Mediterranean basin (IPCC 2013), which may  
508 decrease forest cover and food resources (key factors for deer habitat selection;  
509 Jedrzejewska *et al.* 1994; Borkowski & Ukalska 2008) at lower elevations.

510 Modeled effects of precipitation generally dominate over herbivory effects across  
511 plots. It is important to note that we assess the impact of herbivory on annual height-growth  
512 rates and that the accumulated effect of herbivory in total height growth for the study period  
513 would be probably greater than the effect on annual rates averaged over years.  
514 Nevertheless, in the plot with the highest herbivory intensity, the recorded effect of  
515 herbivory was greater than precipitation effect for the whole study period. This  
516 demonstrates the capacity of ungulate browsing to counteract the beneficial effect of  
517 climate, as has been previously observed in other ecosystems different from Mediterranean  
518 ones (e.g. Speed *et al.* 2011a; Fisichelli, Frelich & Reich 2012).

519 Interestingly, the relative impact of herbivory and precipitation displayed a clear  
520 variability across time. The decrease in the effects of precipitation during the later years of  
521 the series suggest a greater capacity to access water in deeper soil horizons with increasing  
522 sapling size. In contrast, the increase of herbivory effects seems mediated by the rise of the  
523 ungulate population and subsequent increase in herbivory intensity, although the browsing  
524 likelihood for a tree sapling decreased with height as saplings grow (Zamora *et al.* 2001;  
525 Speed *et al.* 2011b). In this context, the time-varying approach, which explicitly consider  
526 temporal variability in the modeled effects, greatly improves the assessment of the effects  
527 of precipitation and herbivory on plant growth accounting for the ontogenetic process of  
528 juvenile maturation and deer population dynamics. Due to the growing interest in climate-  
529 induced vegetation shifts, long-term studies analyzing tree sapling growth prior to their

530 inclusion in the overstory layer are increasingly necessary, which need to include the  
531 temporal variability of the environmental variables affecting tree growth.

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

545 At the treeline, the effect of precipitation on plant performance was much higher  
546 than at woodland. This suggests that the treelines are responsive zones to climatic  
547 conditions, in agreement with previous studies (e.g., Harsch *et al.* 2009; Speed *et al.*  
548 2011a,b). The increasing warmer conditions in the study area (Herrero, Rigling & Zamora  
549 2013; Matías & Jump 2015) could allow for the positive influence of precipitation in this  
550 harsh environment. Thus, strong effects of precipitation and weak influence of herbivory  
551 could allow tree upward expansion, although increasing browsing damages associated to  
552 increments in ungulate population and/or climatic change might limit positive climatic  
553 responses of pine-saplings in the near future.

554           The effects of herbivory presented larger variability among individuals than the  
555 effects of precipitation, since individual pines showed effects of the same sign more  
556 consistently for precipitation. The overall stronger impact of precipitation and its lower  
557 variability between individuals suggests a more pervasive effect of precipitation at the  
558 population level, since all saplings are subjected to similar water availability. In contrast,  
559 the greater inter-individual heterogeneity in the effects of herbivory is consistent with the  
560 different levels of browsing damage between individuals, in agreement with the  
561 hierarchical foraging of mammal herbivores, which includes the individual scale (Danell &  
562 Bergström 2002). In fact, while some individuals escaped ungulate herbivory by reaching  
563 browsing-free height or by the protection of spiny and/or unpalatable shrubs (e.g. *Berberis*  
564 sp. or *Juniperus* sp.), others remained under the browsing threshold or lacked the protection  
565 of shrubs, thus suffering heavy damage. In this context, herbivory can act as a spatially  
566 aggregating force, creating regeneration hotspots associated with low herbivory, and  
567 patches of blocked or slowed-down regeneration associated with high herbivory.

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



578 Overall, our study highlights the benefits achieved by modeling ecological  
579 processes at the individual level and allowing for time-varying effects. Precipitation  
580 fluctuations showed a more pervasive and spatially homogenous effect than did herbivory  
581 on long-term height-growth rate. By contrast, herbivory exerted a more spatially  
582 heterogeneous effect through individual-level damage, producing a negative impact on  
583 plant growth that can constrain treeline shifts when herbivore density is high (Speed *et al.*  
584 2011a,b; Van Bogaert *et al.* 2011). Our results serve to delineate a prediction framework for  
585 treeline shifts under a global warming scenario, based on the relative effects of climate and  
586 herbivory. On one hand, where climate is the dominant environmental factor (and herbivory  
587 pressure is low), the treeline would gradually shift upwards through a spatially  
588 homogeneous altitudinal ascension of saplings. On the other hand, where the effect of  
589 herbivory is more important than climate, herbivory would constrain the growth of  
590 saplings, precluding the upward shift of treeline in many areas, except in patches with low  
591 herbivory, resulting in a spatially heterogeneous vegetation structure. Further studies are  
592 necessary to test these predictions, considering individual-level and temporal heterogeneity  
593 in environmental responses and treeline dynamics. Finally, modeling approaches  
594 considering individual variability would be particularly useful to assess the importance of  
595 other biotic interactions, such host-parasite relations (e.g. mistletoe) or insect herbivory  
596 (e.g. pine processionary caterpillar), on tree species performance. Enhancing our  
597 knowledge about the relative importance of biotic interactions on plant performance and the  
598 spatial scale at which interactions exert influence, would improve the forecasting of  
599 climate-driven vegetation shifts under the global warming scenario.

600

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612

### 613 **Data Accessibility**

614 The data used in the paper will be publicly available on the date of the potential publication  
615 of the paper at Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.kf575>

616

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**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. The standardized modelled effects (mean  $\pm$  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 datasets. 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

Plot	Parameters	Effects	Modelled effects			$R^2$	PMSE	DIC
			Herbivory	Precipitation	Stochasticity			
<b>Fonfría treeline</b>	<b>Constant</b>	<b>IBM</b>	0.009 (0.121)	0.428 (0.108)	1.071 (0.110)	0.314	0.639	1209.0
		<b>LME</b>	0.001 (0.120)	0.419 (0.101)	0.768 (0.055)	0.242	0.712	1097.0
	<b>Time-varying</b>	<b>IBM</b>	-0.002 (0.046)	0.383 (0.079)	1.056 (0.152)	0.674	0.305	955.4
		<b>LME</b>	-0.013 (0.114)	0.383 (0.192)	0.581 (0.048)	0.476	0.494	<b>934.7</b>
<b>Boleta treeline</b>	<b>Constant</b>	<b>IBM</b>	-0.025 (0.034)	0.348 (0.054)	1.156 (0.105)	0.252	0.701	1529.0
		<b>LME</b>	-0.024 (0.031)	0.340 (0.046)	0.889 (0.056)	0.121	0.825	1425.0
	<b>Time-varying</b>	<b>IBM</b>	0.010 (0.037)	0.388 (0.077)	1.049 (0.146)	0.684	0.295	<b>1163.0</b>
		<b>LME</b>	0.041 (0.080)	0.451 (0.192)	0.773 (0.053)	0.296	0.659	1299.0
<b>Fonfría woodland</b>	<b>Constant</b>	<b>IBM</b>	-0.244 (0.203)	0.322 (0.150)	1.110 (0.101)	0.278	0.678	1469.0
		<b>LME</b>	-0.205 (0.194)	0.246 (0.159)	0.854 (0.056)	0.158	0.789	1360.0
	<b>Time-varying</b>	<b>IBM</b>	-0.198 (0.130)	0.329 (0.104)	1.058 (0.145)	0.639	0.339	<b>1094.0</b>
		<b>LME</b>	-0.237 (0.207)	0.333 (0.194)	0.781 (0.060)	0.280	0.677	1203.0

<b>Boleta woodland</b> <i>(P. sylvestris)</i>	<b>Constant</b>	<b>IBM</b>	-0.173 (0.044)	0.263 (0.044)	1.236 (0.063)	0.182	0.767	4463.0
		<b>LME</b>	-0.172 (0.040)	0.265 (0.039)	0.904 (0.034)	0.099	0.844	4032.0
	<b>Time-varying</b>	<b>IBM</b>	-0.186 (0.060)	0.146 (0.052)	1.081 (0.087)	0.662	0.317	<b>3249.0</b>
		<b>LME</b>	-0.211 (0.115)	0.091 (0.132)	0.790 (0.034)	0.248	0.706	3383.0
<b>Boleta Woodland</b> <i>(P. nigra)</i>	<b>Constant</b>	<b>IBM</b>	0.012 (0.036)	0.232 (0.040)	1.232 (0.082)	0.188	0.761	2709.0
		<b>LME</b>	0.012 (0.030)	0.228 (0.035)	0.954 (0.047)	0.052	0.888	2511.0
	<b>Time-varying</b>	<b>IBM</b>	0.001 (0.053)	0.209 (0.050)	1.115 (0.107)	0.630	0.347	<b>2003.0</b>
		<b>LME</b>	0.050 (0.097)	0.221 (0.080)	0.953 (0.054)	0.109	0.836	2341.0

791

792 **Figures**

793

794 **Fig. 1.** A graphical representation of the individual-based hierarchical Bayesian time-series  
795 model (Individual-Based Model; IBM) linking the dynamic variables used in the analysis,  
796 each belonging to an ecological scale. Black unidirectional arrows connecting the boxes  
797 denote a statistical effect modeled; the parameters measuring these effects are depicted  
798 along with its corresponding arrow. Grey arrows denote a stochastic effect affecting a given  
799 variable.  $r$ ,  $K$ : intrinsic rate of increase and carrying capacity of red deer population,  
800 respectively;  $\Sigma_{n_i}$ : process variance of the stochastic term for the environmental and  
801 demographic process error of the Gompertz kernel used to model the evolution of red deer  
802 population;  $\tau_{n_i}^2$ : sampling variance of the Gaussian model used to link population estimates  
803 to the true abundances of red deer;  $\varphi_k$ ,  $\zeta_k$ : effects of red deer abundance and summer  
804 precipitation, respectively, on herbivory intensity (estimated as the proportion of saplings  
805 with the leader shoot browsed for each plot and species);  $\sigma_{h_i}^2$ : variance of the  
806 environmental noise term of the modeled herbivory intensity;  $\mathbf{a}_k$ ,  $\mathbf{b}_k$ : the intercept and the  
807 slope, respectively, of the regression model used to subtract the biological trend in Relative  
808 Height Growth (RHG) due to the aging of pines;  $\beta_{k,t}$ : column vector including the time-  
809 varying individual-level parameters estimating the temporal effect of herbivory on  
810 individual pines;  $\gamma_{k,t}$ : column vector including the time-varying individual-level parameters  
811 estimating the temporal tracking of lagged summer precipitation by individual pines.  $\sigma_{x_{i,t}}^2$ :  
812 variance term for the environmental stochasticity impacting on residual RHG (rRHG). See  
813 text for further details.

814

815 **Fig. 2.** Time-series of Relative Height Growth (RHG), precipitation variability, red deer  
816 population size and herbivory intensity in the study area from 1992 to 2008. a) Value of

817 RHG for each individual pine sapling and year, pooled across the four plots and two species  
818 (*Pinus sylvestris* and *P. nigra*). The thick red line is a locally-weighted least-squares  
819 function fitted to enhance the local dynamics. b) Time series of precipitation during  
820 summer (months of June, July and August). c) Estimations of red deer abundance across the  
821 landscape based on observed yearly abundance (counts) are shown as open green squares;  
822 the latent (unobserved) states estimated with the Gompertz state-space model is shown as a  
823 solid red line, with 95% credible intervals depicted as dotted red lines. d) Recorded  
824 proportion of saplings with the leader shoot browsed for each plot and species during the  
825 study period (1993-2008).

826

827 **Fig. 3.** Plots of time-varying coefficients measuring the effect of herbivory intensity,  
828 precipitation variability and environmental stochasticity on residual Relative Height  
829 Growth of *Pinus sylvestris* in the treelines of Boleta and Fonfría. The effects shown are the  
830 individual-averaged time-varying impact of herbivory, summer precipitation, and  
831 environmental stochasticity. For each graph, the dotted lines represent the 68% credible  
832 interval, equivalent to 1 standard deviation, while the thick red lines represent the fitting of  
833 a Linear Mixed-Effects (LME) model to the data.

834

835 **Fig. 4.** Plots of time-varying coefficients measuring the effect of herbivory intensity,  
836 precipitation variability and environmental stochasticity on residual Relative Height  
837 Growth of *Pinus sylvestris* in the woodlands of Fonfría and Boleta and *P. nigra* in Boleta  
838 woodland. The effects shown are the individual-averaged time-varying impact of herbivory,  
839 precipitation, and environmental stochasticity. For each graph, the dotted lines represent the  
840 68% credible interval, equivalent to 1 standard deviation, while the thick red lines represent  
841 the fitting of a Linear Mixed-Effects model (LME) to the data.

842 **Fig. 5.** Posterior simulated (predicted) datasets of residual Relative Height Growth (rRHG)  
843 obtained with the constant and time-varying parameters models for both the Individual-  
844 Based Model (IBM, purple and red open circles for the constant and time-varying model,  
845 respectively) and the Linear Mixed-Effects model (LME, green and blue open circles, for  
846 the constant and time-varying model, respectively). These values were plotted against the  
847 observed rRHG, pooled for the four plots and the two species (*Pinus sylvestris* and *P.*  
848 *nigra*). Each dot represents the average of 1000 synthetic values randomly obtained with  
849 each fitted model (standard errors omitted for clarity). The thick black line is the Y=X  
850 regression line. Note data standardization prior to the analyses.

851

852

853

854 **SUPPORTING INFORMATION**

855 Additional supporting information may be found in the online version of this article:

856

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

859

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

863

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

867

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

869

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

871

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

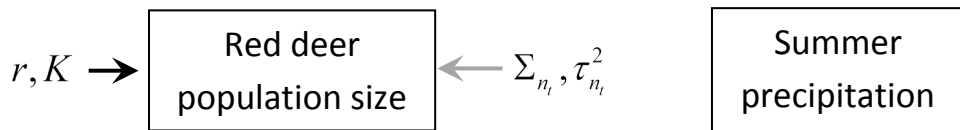
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875 **Appendix S4** BUGS code for the fitting of the Linear Mixed-Effect Model with constant  
876 parameters.

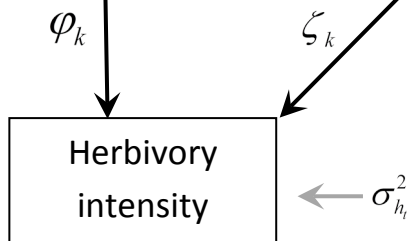
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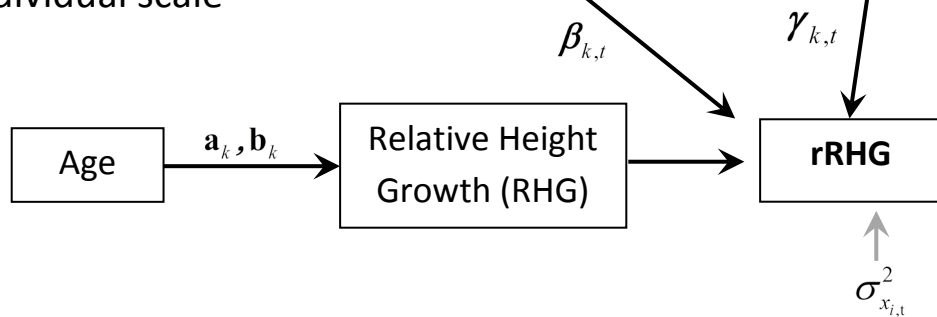
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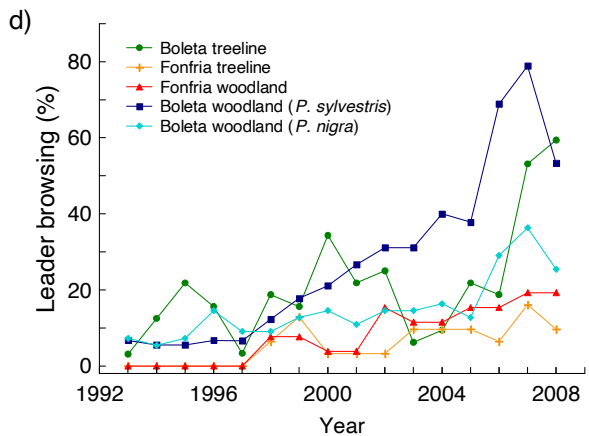
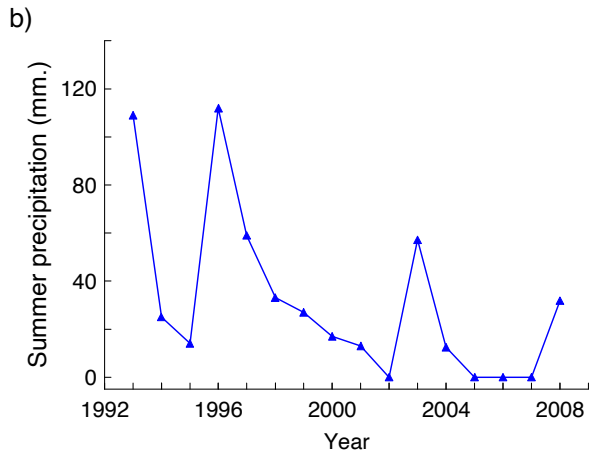
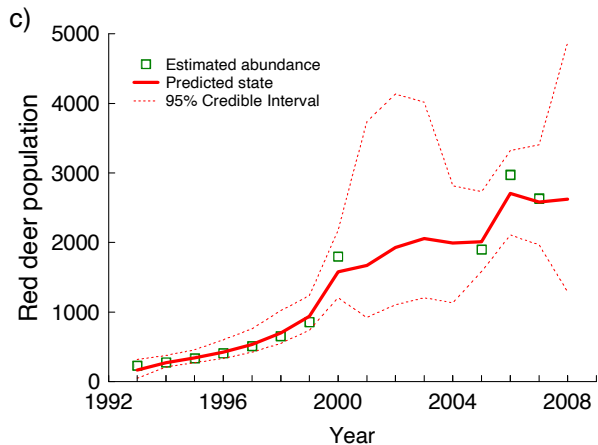
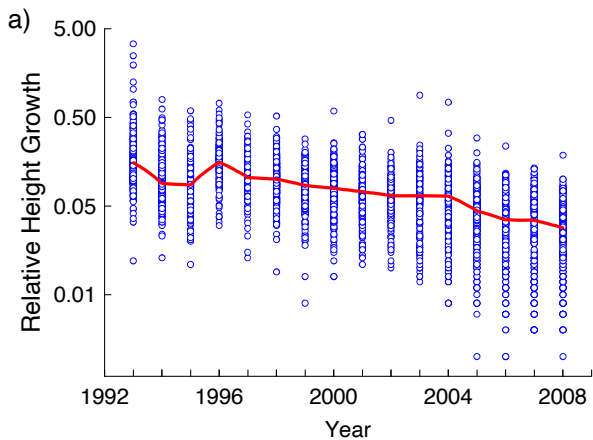
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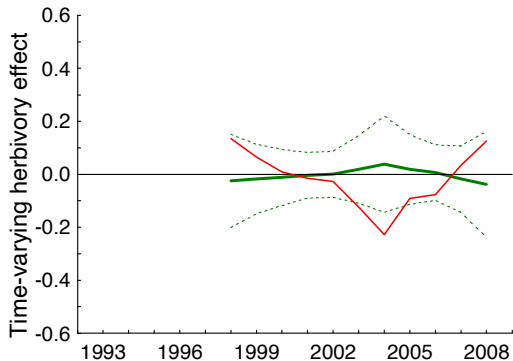
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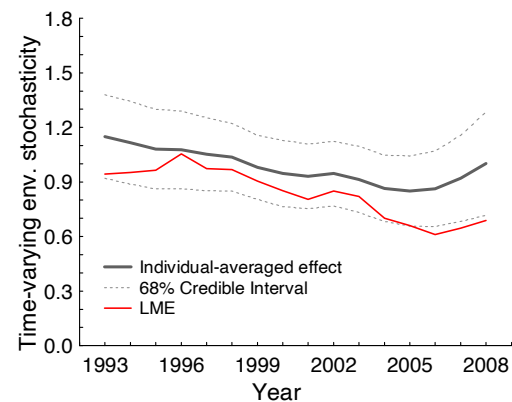
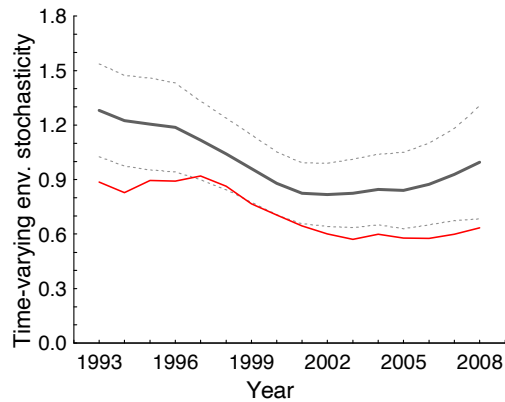
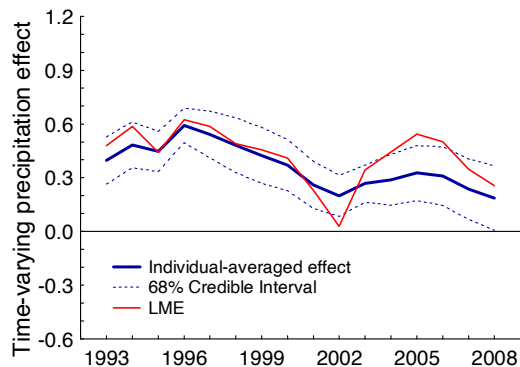
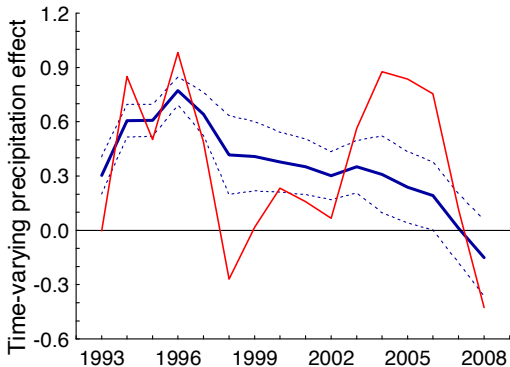
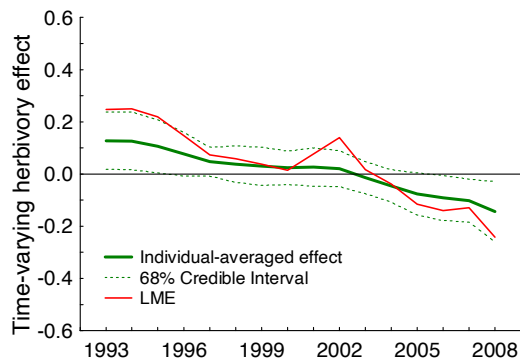




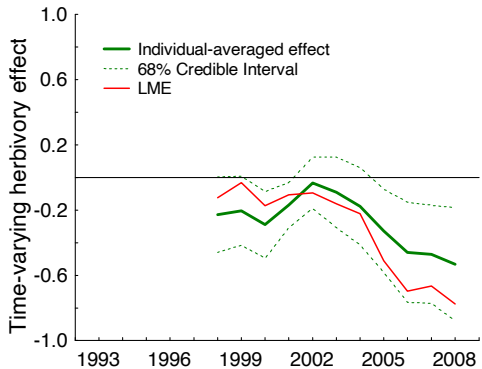
## Fonfría



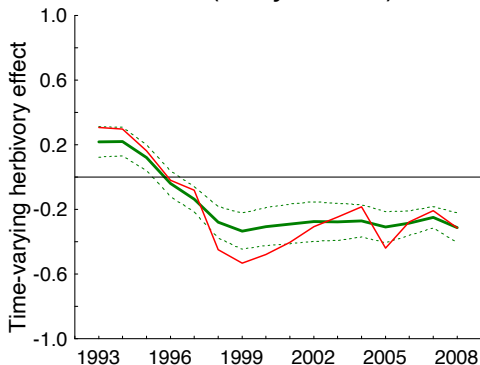
## Boleta



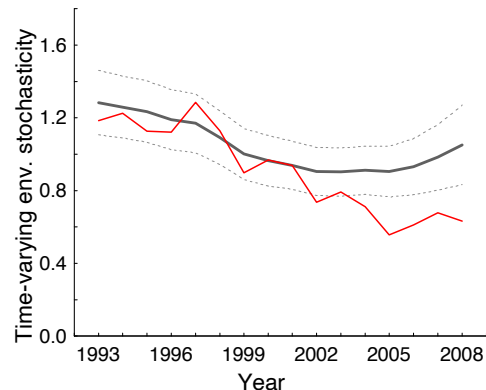
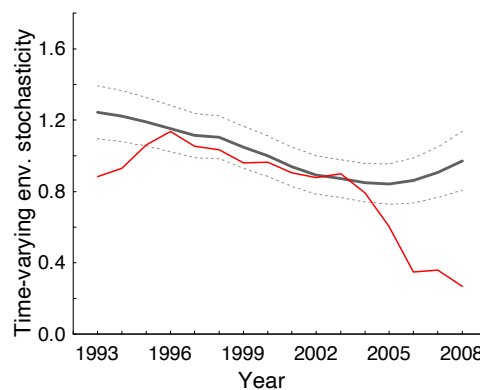
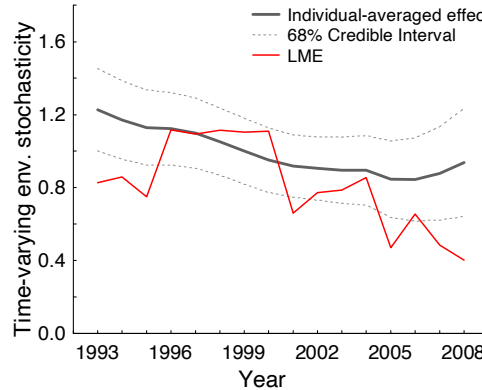
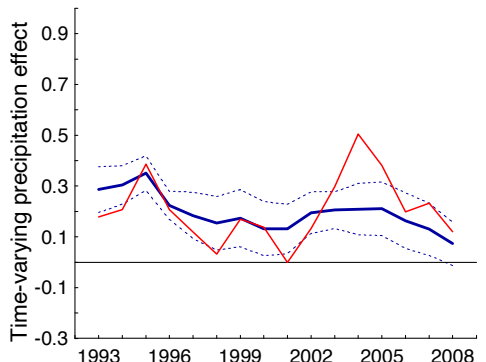
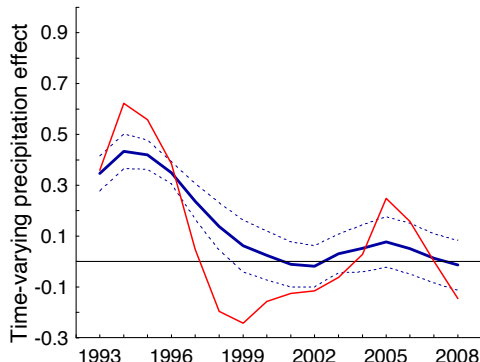
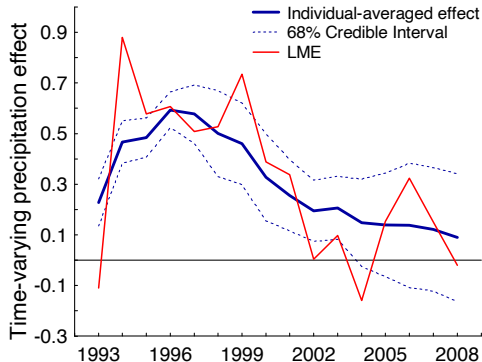
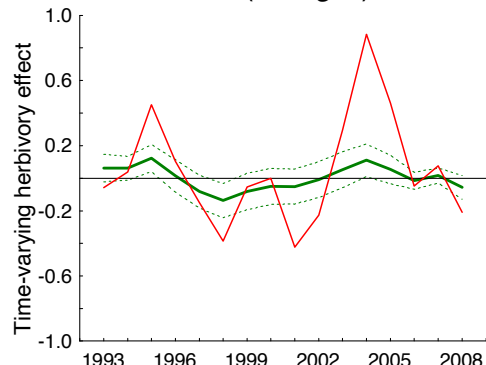
### Fonfría



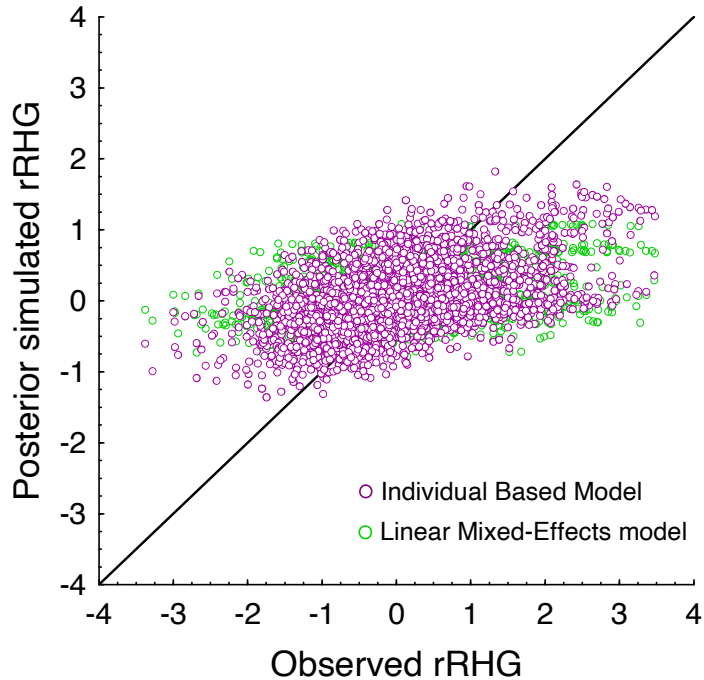
### Boleta (*P. sylvestris*)



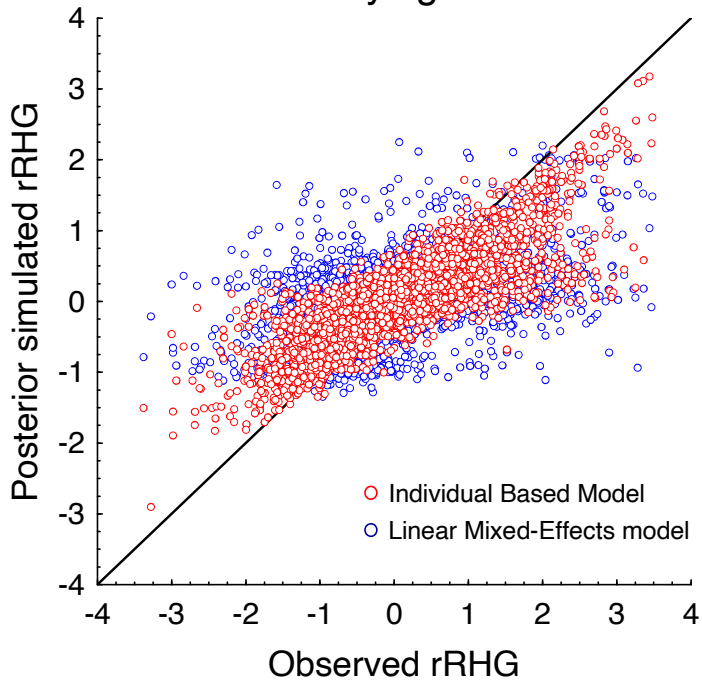
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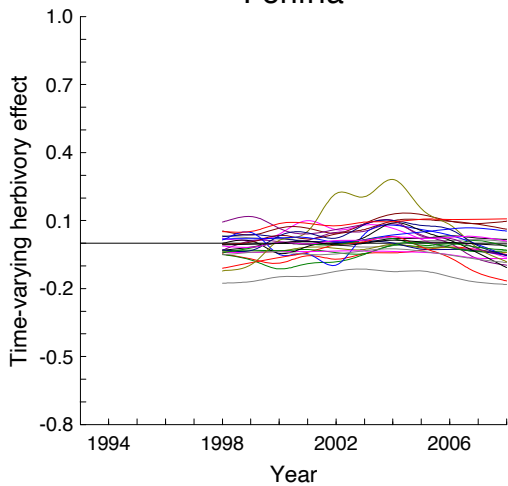
### Constant models



### Time-varying models



## Fonfría



## Boleta

