

1 **Survival vs. growth trade-off in early recruitment challenges global warming**
2 **impacts on Mediterranean mountain trees**

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25 **Abstract**

26 Climate change is expected to alter the geographic distribution of many plant species
27 worldwide. However, there is still no clear evidence showing a generalized direction and
28 magnitude of these distribution shifts. Here, we have surveyed, in nine mountainous
29 regions in Spain, an array of tree species along entire elevational ranges, as surrogates of
30 their global climatic ranges, to test for elevational shifts towards cooler locations. We
31 analysed the distribution recruitment patterns of five dominant tree species, recording the
32 abundance and measuring the primary growth of juveniles in 306 plots. Three of the
33 species have a temperate-boreal distribution with populations at their southern edge in the
34 Mediterranean mountain ranges: *Pinus sylvestris*, *P. uncinata* and *Fagus sylvatica*; and
35 the other two species have a Mediterranean distribution: *Quercus ilex* and *P. nigra*.
36 Despite the contrasting phylogenies and biogeographies, we identified a similar pattern in
37 recruitment abundance across species, with an asymmetric distribution of juveniles (more
38 recruits in the middle-upper elevation of their range), but higher annual growths at lower
39 elevations. This survival-growth trade-off at the early recruitment stage may potentially
40 counterbalance at population level the negative effect of global warming on recruit
41 survival at the lower edge of species ranges. These findings suggest a demographic
42 stabilisation process at the early recruitment stage of these tree species, and highlight the
43 importance of considering the different demographic stages across the whole climatic
44 range to understand the effects that climate change may exert on species distributions and
45 population dynamics.

46

47 **Key words:** climate change; climatic gradient; demographic stabilising processes;
48 elevational shift; forest regeneration; Mediterranean forests; species distribution.
49

Accepted version

Abbreviations: Sampled transects' position along elevational gradients: U: upper, MU: mid-up, M: middle, ML: mid-low, L: lower transects. Se: seedlings emerged during the current growing season; S1: saplings from one to five years; S2: saplings over five years.

50 **Introduction**

51 An increasing number of studies are showing latitudinal and elevational shifts of many
52 species in response to climate change (Parmesan and Yohe, 2003; Rabasa et al., 2013).
53 Although changes in traditional land uses contribute to some of these species distribution
54 shifts (Peñuelas and Boada, 2003; Batllori and Gutiérrez, 2008; Ameztegui et al., 2010),
55 most of the studies have suggested that global warming and the increased frequency of
56 extreme climatic events are the main causes of gradual upward and poleward movements
57 and consequent changes in the species composition of ecosystems (Wardle and Coleman,
58 1992; Peñuelas and Boada, 2003; Thuiller et al., 2005; Beckage et al., 2008; Bertrand et
59 al., 2011b; Benavides et al., 2013; Matías and Jump, 2014). However, this evidence runs
60 in parallel with other studies showing a lack of species distribution changes (Lenoir et al.,
61 2009, 2010), species that have increased their cover and/or abundance with rising
62 temperature or aridity (Wang et al., 2006; Gimeno et al., 2012) or even that have
63 experienced a downslope range displacement (Lenoir et al., 2010; Crimmins et al. 2011;
64 Rabasa et al., 2013).
65 Lloret et al. (2012) shed some light on these apparent contradictions suggesting that some
66 stabilising demographic processes may mitigate or compensate the negative effects in
67 plant communities induced by extreme climate events (Table 1). Within the mitigation
68 category, local factors (both biotic, like facilitation, and abiotic, like physiography or site
69 quality) may provide microrefugia and attenuate the direct negative effects of a changing
70 climate on individuals (Pearson and Dawson, 2003; Araújo and Luoto, 2007; Dobrowski,
71 2011; McLaughlin and Zavaleta, 2012). Moreover, species-specific characteristics related
72 to their adaptation or acclimation ability may also buffer the expected climatic impacts on
73 populations (Aitken et al., 2008; Nicotra et al., 2010; Richter et al., 2012). Accordingly,
74 recent studies have suggested that the direct impacts of global warming may be smaller

75 than predicted, and have shown a high degree of homeostasis in different processes of
76 some species in response to increasing temperatures (Gunderson et al., 2011; Baldi et al.,
77 2012). Within a second category of compensatory processes, Lloret et al. (2012) included
78 the beneficial effect that warmer temperatures may have over some life cycle stages and
79 ecological processes. For instance, an increase in growth with temperature may
80 compensate a lower seedling survival (Doak and Morris, 2010); or reduce current
81 competitive or antagonistic interactions (McDowell et al., 2006; Carnicer et al., 2011),
82 and increase mutualistic relationships (Le Conte and Navajas, 2008; Giménez-Benavides
83 et al., 2011).

84 The mismatch between both types of observational outcomes (shift *vs.* no-shift) may not
85 only reflect the species-specific characteristics, but also differences in the spatial and
86 temporal study scales. Undoubtedly, some species are more vulnerable to environmental
87 changes and will respond earlier than others. Nevertheless, the studies showing shifts
88 have been frequently conducted considering a single species or population, or have been
89 focused on changes occurring at the edge of species ranges, being then unable to reveal
90 the whole picture by neglecting the overall distribution of the species (but see these
91 studies with waterbird species -Lehikoinen et al., 2013- and stream fish species -Comte
92 and Grenouillet, 2013-). Thus, it is a priority to conduct more comprehensive studies in
93 which a set of species are simultaneously surveyed at several spatial scales, covering their
94 whole distribution range (Lenoir and Svenning, 2015), and including different life stages
95 (*i.e.* including the regeneration niche, see Grubb, 1977). This will shed light on the
96 demographic mechanisms and trade-offs involved in the shift *vs.* no-shift responses, and
97 will help to identify global responses to current warming and design strategies to mitigate
98 its impact over plant communities.

99 In this study, we contribute to this goal and we analyse the distribution of the recruitment
100 (seedlings and saplings), in terms of abundance and primary growth, of four dominant
101 tree species, surveying their entire elevational range in Mediterranean mountains, as a
102 surrogate of the climatic range that each species experiences along their latitudinal
103 distributions. Using elevation as a surrogate for climate range is a useful tool to study
104 responses under different climatic scenarios within a single population and, therefore,
105 minimising differences due to genetic variability, compared to surveys carried out in
106 large areas, and therefore, including different populations (Ruíz-Benito et al., 2012;
107 Vayreda et al., 2013; Carnicer et al., 2014). Three of the target species have a temperate-
108 boreal distribution with populations at their global southernmost limit in the Iberian
109 mountain ranges: Scots pine (*Pinus sylvestris* L.), mountain pine (*Pinus uncinata*
110 Ramond ex DC.) and European beech (*Fagus sylvatica* L.); and the other one has a
111 Mediterranean distribution: Iberian black pine (*Pinus nigra* Arn. ssp. *salzmannii* (Dunal)
112 Franco). Another Mediterranean dominant tree species was included in the target species
113 pool of this study due to its great relevance in the Iberian Peninsula: holm oak (*Quercus*
114 *ilex* L.). However, this species was not surveyed along its entire elevational range and its
115 trailing edge was left out, because this species has no low elevational limit in the
116 Mediterranean mountains. Our main aim is to test in the study populations whether there
117 is an overall, pervasive elevational shift of the young cohorts towards cooler locations
118 within the entire elevational range of the adult, which would be transferable to poleward
119 shifts in response to the ongoing climate change, or if the altitudinal patterns are species-
120 specific (Lenoir et al., 2009; Woodall et al., 2009). We expect that the recruits of the
121 Mediterranean species, better adapted to summer drought, would be less affected by the
122 ongoing climate change and be more abundant near their central part of the elevational
123 range, where the density of conspecific adults and, therefore, seed rain are greater than at

124 the edges of their range. By contrast, we expect that the species with populations at their
125 trailing edge of their distribution, therefore marginal populations, would show shifts of
126 their optimum juvenile abundance towards higher elevations (Matías and Jump, 2014).
127 This outcome would show the different climatic conditions imposed by the global
128 warming between the conditions when the current adult stand established, and the present
129 situation. Hence, we hypothesise an idiosyncratic response of the different species with
130 no general upward trend, and where a potential compensatory process enhancing the
131 performance of the juveniles under warmer conditions may be relevant, especially for
132 those species whose populations are at their southern limit.

133

134 **Material and Methods**

135 *Study sites*

136 The study was conducted in nine mountain ranges across Spain during the early summer
137 in 2010 and 2011 (Fig. 1). The entire sampling required two years due to the short lapse
138 of time between the emergence of most of the seedlings and the onset of the summer
139 drought. For every species we sampled two natural pure stands located in different
140 mountain ranges (three in the case of *P. sylvestris*), making a total of 11 study sites (see
141 Supporting Information, Appendix Table A.1). These stands showed neither visible signs
142 of being planted, nor any evidence of management that could affect the current
143 recruitment. Within each site, five transects were established at five elevational levels
144 (Fig. 1). The upper (U) and the lower (L) transects were placed in the ecotones of each
145 target species with the adjacent communities, and considered front and rear edges of their
146 range respectively. In the majority of the cases, U transects were located at the treeline
147 (*i.e.* transition from the uppermost closed forests to the treeless mountainous vegetation).
148 The three intermediate levels: mid-low, middle and mid-up levels (henceforth ML, M,

149 and MU respectively) were evenly located within the elevational range of each species,
150 with at least 100 m difference in elevation among them, being ML and MU located near
151 the boundary with the ecotones (Fig. 1). In the case of *Q. ilex*, we only considered the
152 three superior levels since this species has no low elevational limit in the Iberian
153 Peninsula. Therefore, there was a total of 51 transects sampled ([3 species * 2 sites * 5
154 transects] + [1 species * 3 sites * 5 transects] + [1 species * 2 sites * 3 transects]).

155

156 *Recruitment sampling and environmental variable recording*

157 We established six plots (4 x 4 m) within each transect, that is 306 plots in total (51
158 transects * 6 plots), separated by at least 100 m (Fig. 1). Three plots per transect were
159 haphazardly located under fully canopied stands, and the other three in small forest gaps
160 to include contrasting conditions within each forest and elevation, avoiding ravines,
161 boulders, cliffs or other geomorphologic elements which could bias our measurements
162 ameliorating the effect of climate by local physiography (Dobrowski, 2011). In every plot
163 we recorded the number of recruits by counting the seedlings recently emerged and
164 saplings (up to 1.50 m tall). Seedlings and saplings of resprouting species (*Q. ilex* and *F.*
165 *sylvatica*) were correctly identified from vegetative offsprings following Espelta et al.
166 (1995). We estimated the age of the recruits by counting the terminal bud scars
167 (internodes) along the main stem and we sorted them into three different age classes
168 (Espelta et al., 1995), assuming a different sensitivity to the environment (Collins and
169 Carson, 2004): Se: seedlings emerged during the current growing season and without bud
170 scars; S1: saplings from one to five years, that had thus experienced at least one summer
171 drought and one winter; and S2: saplings over five years. The age of the individuals
172 included in the last category was not fully dated due to the difficulty with distinguishing
173 scars in the field as individuals grow and become woodier, but it was verified that they

174 exceeded 5 years. We also measured the primary shoot growth in previous years (growths
175 occurred in 2007, 2008 and 2009) and averaged them, as a proxy of their individual
176 performance. We identified the current shoot (not considered for the study because the
177 growing season was not finished when the sampling took place) and measured the length
178 of the previous internodes along the main stem not damaged by herbivores. The existing
179 literature demonstrated that shoot growth is a good indicator of environmental
180 favourability (Willms et al., 1998), as well as the impact of drought conditions on plant
181 growth (Mutke et al., 2003; Peñuelas et al., 2004; Thabeet et al., 2009).

182 Some biotic and abiotic environmental variables were assessed in each plot. All adult
183 trees within a 10 m radius around the regeneration plot were mapped and their diameter at
184 breast height -dbh- was measured. Afterwards we calculated the basal area (both
185 considering every adult tree and only the conspecific individuals) and tree density of
186 adult trees of the target species in each plot. Finally, we translated the elevation and
187 latitude of every plot (through the GPS coordinates) into climatic variables using the
188 Climatic Digital Atlas of the Iberian Peninsula (Ninyerola et al., 2005) (see Appendices
189 Table A.1. and Figure A.1.).

190

191 *Data filtering and statistical analysis*

192 The abundance of the individuals of each species and age class along the elevation and
193 temperature ranges was compared using the Kruskal-Wallis test. However, as the amount
194 of seedlings (Se) varies greatly among years, we considered only the saplings (S1 and S2)
195 for further analyses, *i.e.* survivors after the first summer drought, which is considered the
196 main bottleneck for recruitment in Mediterranean areas (Jordano and Herrera, 1995;
197 Castro et al., 2004; Giménez-Benavides et al., 2007; Linares and Tíscar, 2010).

198 We analysed the variation of the regeneration pattern along the elevational gradient.
199 Hence, we compared our response variables along the five elevational levels (fixed
200 variable) using Generalized Linear Models (GLM; McCullagh and Nelder, 1989) and
201 Generalized Linear Mixed Models (GLMM; Breslow and Clayton, 1993). For the
202 response variable *abundance of saplings* per species and at plot level (age class was
203 neglected due to the low figures in some transects of these count data), we run GLMs and
204 assumed a negative binomial distribution and a log link function. We selected this
205 distribution after noticing the presence of over-dispersion (McCullagh and Nelder, 1989;
206 Hoef and Boveng, 2007). In addition to *elevational levels*, two covariates describing the
207 structure of the adults within a plot, therefore related to the seed rain, were considered to
208 fit the models: *tree density* and *mean dbh* of conspecific adult individuals (Vayreda et al.,
209 2013; Matías and Jump, 2014). Finally, the variable *site* was treated as a fixed factor due
210 to the low number of levels (two/three for each species) to be considered a random effect
211 (Crawley, 2002; Bolker et al., 2008).

212 The other response variable, the *individual mean growth* per species and age class along
213 elevational levels was log-transformed and analysed assuming a normal distribution and
214 an identity link function, using a mixed approach (GLMM). This time the sample size
215 (data at individual level) allowed us to consider the age class, and a model for each age
216 class was run separately. Light availability is one of the best predictors for saplings'
217 growth (Gómez-Aparicio et al., 2008; Benavides et al., 2013). Therefore, this time the
218 total *basal area* of the plot was included as a covariate, considered as an index of
219 competition for light with adult trees (Urbieta et al., 2011). Concerning the random
220 variables, we considered the hierarchical structure of the data, with likely different level
221 of correlation among observations from the same *site* and *plot* (nested design).

222 To analyse the overall trend in the regeneration pattern across the different elevational
223 levels, and make the data from different species comparable, we standardised the
224 abundance and growth values per species, *i.e.* we subtracted from each value the species
225 averaged abundance or growth, respectively, and divided it by the standard deviation.
226 Then, we pooled the data and compared them along the elevation gradient (levels) using a
227 GLMM. Similar to the analyses conducted per species, for abundance data we included
228 the covariates *density* and *mean dbh*. This time *site* was considered a random variable
229 (with 11 levels), and we assumed a gamma distribution and a log link function (after
230 adding two units to the standardised data to avoid negative values). For growth data we
231 assumed a normal distribution, and we considered *basal area* as a covariate, and *plot*
232 within *site*, as random factors.

233 We tested for significance of fixed effects comparing models with likelihood ratio tests,
234 and we removed the covariates if they did not significantly improve the fits. The
235 estimation of the parameters was done through Maximum Likelihood analyses for the
236 GLMs, and for comparison between models with the same random structure (GLMMs),
237 and through the Restricted Maximum Likelihood approach for assessing the parameters
238 of the final selected GLMMs.

239 Finally, we implemented the Tukey's post-hoc test (Games and Howell, 1976) to
240 examine significant differences in abundance and growth along the elevational levels for
241 every single species and globally (*i.e.* for pooled standardised data). The GLMs and
242 GLMMs were performed using packages MASS (Venables and Ripley, 2002), nlme
243 (Pinheiro et al., 2013) and stats (R Team 2014) in R (R Core Team, version 3.0.2, 2013).

244 **Results**

245 *Distribution of juveniles along the elevation*

246 We recorded a total amount of 9310 juveniles in the 306 plots, sorted into 5283 juveniles
247 of *P. sylvestris*, 547 of *Q. ilex*, 1143 of *P. nigra*, 740 of *P. uncinata*, and 1597 of *F.*
248 *sylvatica*. The distribution of juveniles by age class (Fig. 2) along the elevation and
249 temperature gradients showed a shift towards higher elevations within the elevation range
250 of the adult individuals (therefore, towards cooler temperatures) of the saplings
251 (particularly S1) of *Q. ilex* and pines, compared to the elevation at which most of the
252 seedlings emerged. By contrast, *F. sylvatica* recruits occurred mainly in the lower areas
253 (L), although there was no significant difference among the distributions of the different
254 age classes.

255

256 *Abundance and growth of saplings along elevational levels*

257 Removing the seedlings (Se), the total amount of saplings found in the 306 plots were
258 3191, sorted into 1367 saplings of *P. sylvestris* (surveyed within 90 plots), 543 of *Q. ilex*
259 (within 36 plots), 564 of *P. nigra* (within 60 plots), 608 of *P. uncinata* (within 60 plots)
260 and 109 of *F. sylvatica* (within 60 plots).

261 At tree species level (analyses per species), the GLM showed a similar trend for
262 abundance data of saplings of all species along the elevational levels, with a significant
263 effect but for *P. nigra* (Table 2; Fig. 3). The U and L levels had the lowest saplings
264 abundances. Focusing on the three intermediate elevational levels, all of them showed
265 higher figures in MU than in the ML, with a significant difference for *P. sylvestris* and *F.*
266 *sylvatica*. *Pinus uncinata* and *Q. ilex* had its maximum abundance of saplings at the MU
267 level, showing an abrupt decrease between MU and U levels. Considering pooled data
268 (global analysis), the estimates of the standardised mean abundance of saplings showed a

269 significant difference among elevational levels as well (Table 2; Fig. 3), with the highest
270 number of saplings appearing in the M level, and followed by MU. These numbers were
271 significantly higher than those found at the ecotones (L and U), which accounted for the
272 lowest figures.

273 Concerning the covariates included in the models for abundance estimation (Table 2),
274 significant differences among sites hosting the same species appeared, but for *F.*
275 *sylvatica*. *Tree density* did not appear as an important factor affecting saplings'
276 abundance (except for *P. nigra* with a negative effect), while the mean *dbh* of the adults
277 affected positively the abundance of species with resprouting ability, *i.e.* *F. sylvatica* and
278 *Q. ilex*.

279 Analyses run with mean annual growth data showed a clear decrease in annual growth for
280 younger saplings (S1: from 1 to 5 years) with elevation, particularly when comparing L
281 and ML levels with higher ones, both considering data per species and pooled
282 standardised data. For older juveniles (S2: over 5 years), there was a global slight
283 increase upslope (Table 3; Fig. 4), but there were large differences in the trends of the
284 different species. In addition, a generalized negative effect of the *basal area* appeared
285 affecting annual growth (Table 3), although not significant for every species, and mainly
286 affecting the old saplings (older than 5 years).

287

288

289 **Discussion**

290 Opposite to our hypothesis, and despite the contrasted phylogeny and biogeography of
291 the study species, we identified common patterns in recruitment abundance and growth
292 along climatic gradients for these species. This result is especially relevant when it is
293 considered that recruitment is very dependent on local processes and hence, highly site-
294 dependent (Gómez-Aparicio, 2008; Matías et al., 2011; Ameztegui and Coll, 2013;
295 Benavides et al., 2013). Therefore, this outcome shows the importance that climate exerts
296 as one of the main drivers for seedlings' survival and ingrowth rate (Urbieto et al., 2011;
297 Vayreda et al., 2013; Carnicer et al., 2014).

298 Sapling abundance exhibited a common asymmetric pattern in pine saplings
299 independently of their biogeographical origin, with more saplings in the middle-upper
300 than in middle-lower elevations. As expected, density and basal area of conspecific adults
301 were higher in the three intermediate transects than in the ecotones (Fig. 2; Appendix
302 Figure A.1.), in agreement with the number of saplings. Within these three elevational
303 levels, it is remarkable that, despite the higher abundance of recently emerged seedlings
304 near or even below the middle range transects, sapling abundance was skewed to higher
305 elevations (lower temperatures). Lacking historical records, we cannot completely
306 dismiss that this ontogenetic shift simply renders different requirements for emergence
307 vs. seedling survival (Werner and Gilliam, 1984), regardless of the ongoing climate
308 changes. However, we assumed that this pattern suggests that seedling survival is greater
309 at higher elevations where heat- and drought-stresses are typically lower compared to
310 seedling emergence, supporting the current expectations in response to climate warming
311 (IPCC, 2007; Hughes, 2000). Nevertheless, we recorded the lowest densities at the
312 uppermost transects suggesting that recruitment up there may be hampered, likely, either
313 by climatic variables (not exclusively temperature and precipitation, but also radiation,

314 freezing events, wind, etc.) and other local conditions. Consequently we cannot prove an
315 expansion of the current range limits of the study species beyond their current boundary
316 (upward migration) as other studies did (Peñuelas and Boada, 2003; Peñuelas et al., 2007;
317 Batllori and Gutiérrez, 2008; Jump et al., 2012; Matías and Jump, 2014). In other words,
318 our results agree with an upslope movement of central tendencies of the study species
319 distributions but we had no evidence for an extension of the species ranges upslope
320 (Breshears et al., 2008; Kelly and Goulden, 2008; Lenoir et al., 2008, 2009). Such a
321 statement would have required an additional study focused at the ecotones comparing the
322 sapling abundance of the target species with those from competing species.

323 The results from both *Fagaceae* species were a bit less clear. The elevation range of *Q.*
324 *ilex* sampled in this study only covered the upper edge of its distribution, exhibiting again
325 a decrease of the overall sapling abundance in the U transect. However, looking at the
326 elevational distribution of young saplings (under five years), they were more abundant
327 near the upper ecotone compared to the older saplings, similar to the distribution of pines.
328 This outcome agrees with studies carried out in Spain using data from the National Forest
329 Inventories, showing an upwards shift of *Q. ilex* recruits towards cooler areas, especially
330 relevant in stands where this species adjoins pine forests upslope, a situation that seems to
331 facilitate oak seedlings success (Urbieta et al., 2011; Vayreda et al., 2013; Carnicer et al.,
332 2014). On the other hand, *F. sylvatica* showed an unexpected high density of juveniles at
333 the lower ecotone in our study. This pattern did not match with previous studies
334 conducted in north-eastern Spain, which evidenced an upslope shift of this species during
335 the last century with a consequent species replacement downslope (Peñuelas and Boada,
336 2003; Peñuelas et al., 2007). We posit that other reasons not linked with the species
337 response to climate change may underlie this unexpected trend. In fact, the difference in
338 the stand structure among transects may be interfering with the likely effect of the global

339 warming over the recruitment pattern in the short term. Indeed, the lower transects of
340 these forests showed low densities of bigger adult trees (Appendix Figure A.1.), which
341 means stands with less multi-stemmed individuals. This result matches with the positive
342 effect that *dbh* exerted over the abundance of saplings, likely related to the higher vigour
343 on seed production of one-stemmed individuals from the lower levels compared to the
344 multi-stemmed individuals resulting from old coppicing (Rodríguez-Calcerrada et al.,
345 2011).

346 Moreover, our study reveals opposite trends between recruitment abundance and
347 performance across the elevational range suggesting a potential stabilising process at the
348 population level. Unlike the sapling abundance pattern, mean growth of young saplings
349 (S1) of every target species decreased with increasing elevation. This cohort is known to
350 be more susceptible, not only to the climate and especially to extreme climatic events
351 (Collins and Carson, 2004; Castro et al., 2005), but also to the effect of mammalian
352 herbivores, which can impede regeneration in Mediterranean mountains (Zamora et al.,
353 2001; Herrero et al., 2012). The pattern we found revealed more favourable conditions in
354 warmer places for early recruitment performance, showing the positive role that warm
355 temperatures may exert over growth even in relatively dry Mediterranean areas, when
356 appropriately distributed along the year regarding the annual rainfall distribution, (see
357 Herrero et al., 2013 for secondary growth in adult trees). Similar findings were reported
358 by Doak and Morris (2010) studying the performance of two tundra species along their
359 latitudinal range. They found higher growth rates at the southern edge, despite a lower
360 survival rate of juveniles, suggesting as well a demographic compensatory effect in
361 response to the climate shifts with latitude. Several studies have already reported
362 evidence on the positive correlation between sapling size and their survival, including
363 studies carried out in Mediterranean environments (Cuesta et al., 2010; García-Camacho

364 et al., 2012; Villar-Salvador et al., 2012). Therefore, these higher individual growths of
365 young saplings (more vulnerable) provide more chances to survive because they can
366 overcome quicker this critical stage in terms of climate sensitivity (Pfister 1998; Doak
367 and Morris, 2010) and damage from browsers (Zamora et al., 2001), counterbalancing at
368 the population level the negative effect of global warming over early survival at the
369 trailing edges.

370 Nevertheless, this pattern (higher growths downslope) disappeared as saplings grew,
371 showing again an ontogenetic shift between both cohorts (Werner and Gilliam, 1984),
372 rendering into an idiosyncratic response of juveniles over five years among species and
373 transects. Indeed, several studies have already proved that the niche may change over life
374 cycle due to the different requirements and tolerance to environmental conditions (Miriti,
375 2006; Quero et al., 2008; Soliveres et al., 2010; Bertrand et al., 2011a). This outcome
376 firstly warns about drawing general conclusions about the impact of global warming on
377 plant populations without considering each particular life stage (Grubb, 1977). Moreover,
378 the results hint that once the early seedlings are recruited, the climatic impact on the
379 demography may be somehow attenuated by other factors that become more relevant at a
380 local scale, like the basal area that is considered a proxy for available light. Accordingly,
381 previous studies have supported the non-random effect that local environmental
382 conditions (biotic and abiotic factors) exert over the juveniles' growth, including light
383 availability (Gómez-Aparicio et al., 2008; Matías et al., 2011; Benavides et al., 2013) and
384 plant-plant interactions (Davis et al., 1999; Ameztegui and Coll, 2013; Benavides et al.,
385 2013). In other words, fine scale factors acting hierarchically may exacerbate (for
386 instance, at southern, dry exposures) or mitigate (for instance, by facilitation) the impacts
387 of the changing climate (Lloret et al., 2012).

388 We conclude that our results across entire elevation ranges of different species suggest
389 the existence of a demographic compensation during the early recruitment stage in
390 relation to the global warming impacts. Although in lower (warmer) areas fewer
391 seedlings of different species overcome the first summer drought (*i.e.* main filter in
392 Mediterranean areas), those that survive grow more than those at higher altitudes and
393 would likely move out faster from this highly vulnerable life stage. So, we might expect
394 that the net result turns out in certain stability at the population level, as long as climate
395 change does not exceed certain thresholds. Thus, challenging opportunities arise to
396 explore the persistence and relative importance of these stabilising processes along larger
397 temporal scales, which would allow us to infer how these patterns will evolve as juveniles
398 become adults (*i.e.* paying special attention on the temporal variation of ontogenetic
399 niches shifts), and the role that local factors and management can play on population
400 dynamics under climate change.

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402 **Acknowledgments**

403 The authors thank all the people that made this intensive fieldwork possible, especially to
404 R. Freire, D. López, J. Martínez, A. Rincón, G. Caballé, E. Alquézar, L. Ivorra, S. Martín,
405 C. Rollinson and M. Kaye. We are also very grateful to J. Lenoir and another anonymous
406 referee, whose valuable comments and suggestions have greatly improved the original
407 manuscript. Funding was provided by the Spanish Ministry for Innovation and Science
408 with the grant Consolider-Montes (CSD2008_00040), VULGLO (CGL2010 22180 C03
409 03), MOUNTAINS (CGL-2012-38427), the Community of Madrid grant REMEDINAL
410 2 (CM S2009 AMB 1783) and the European Union with the projects BACCARA (CE:
411 FP7-226299, 7FP) and FunDivEUROPE (CE: FP7-ENV-2010. 265171).

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649

650 **Figure captions**

651 **Figure 1.** Sample design: a) site locations, b) diagram of the transects' layout within a
652 site, and c) display of the plots layout within a transect. Two sites for every species were
653 sampled. Within each location, five transects were established at five elevations: upper
654 (U), mid-up (MU), middle (M), mid-low (ML) and lower (L). MU, M and ML are
655 transects located within the elevational range of a target species in a pure stand, while U
656 and L are located at the ecotones with other communities. Within each transect six plots
657 were established, three of them under fully canopy and the other three in gaps.

658

659 **Figure 2.** Distribution of juveniles along the elevational and climatic gradients (mean
660 annual temperature) of each species by age class, and mean values (standard error) of the
661 plot basal area assessed considering the conspecific adult individuals at the different
662 elevational transects in each type of forest. Age classes were: Se: recently emerged
663 seedlings; not shown for *Q. ilex* due to the small sample size (n=4); S1: saplings from 1
664 to 5 years; S2: saplings over 5 years. Different letters indicate significant differences
665 among the medians of different age classes along the elevational gradient (Kruskal-Wallis
666 test). Dotted lines show the surveyed elevational (climatic) range and the continuous
667 black line the mean elevation (temperature) of the elevational range. Mean annual
668 temperatures were obtained introducing the coordinates of each plot in the Climatic Atlas
669 of the Iberian Peninsula (Ninyerola et al. 2005). U, MU, M, ML, L mean upper, mid-up,
670 middle, mid-low and lower transects respectively

671 **Figure 3.** Estimates of the mean abundance of juveniles according to the elevational
672 level. It was used Generalized Linear Models for the individual species analyses and
673 Generalized Linear Mixed Models for the global analysis (in the latter case the
674 standardised abundance -Std- was used). Thin gray lines show the 95% confidence

675 interval of the estimated means. Elevational transects within every site are (L) lower,
676 (ML) mid-low, (M) middle, (MU) mid-up and (U) upper. Different letters (at the right
677 bottom part of each panel) show the significant differences and *ns* means non-significant
678 differences among elevational levels.

679 **Fig. 4.** Estimates of the mean growth of saplings across the elevational range of pooled
680 data and per species. Analyses run using Generalized Linear Mixed Models, and analysis
681 of pooled data used standardised data -Std-. Thin gray lines show the 95% confidence
682 interval of the estimated means. Elevational transects within every site are (L) lower,
683 (ML) mid-low, (M) middle, (MU) mid-up and (U) upper. Saplings' age class: S1: 1-5
684 years; S2: >5 years. Different letters (legend) show the significant differences, and *ns*
685 means non-significant differences, among estimated means among elevational levels.

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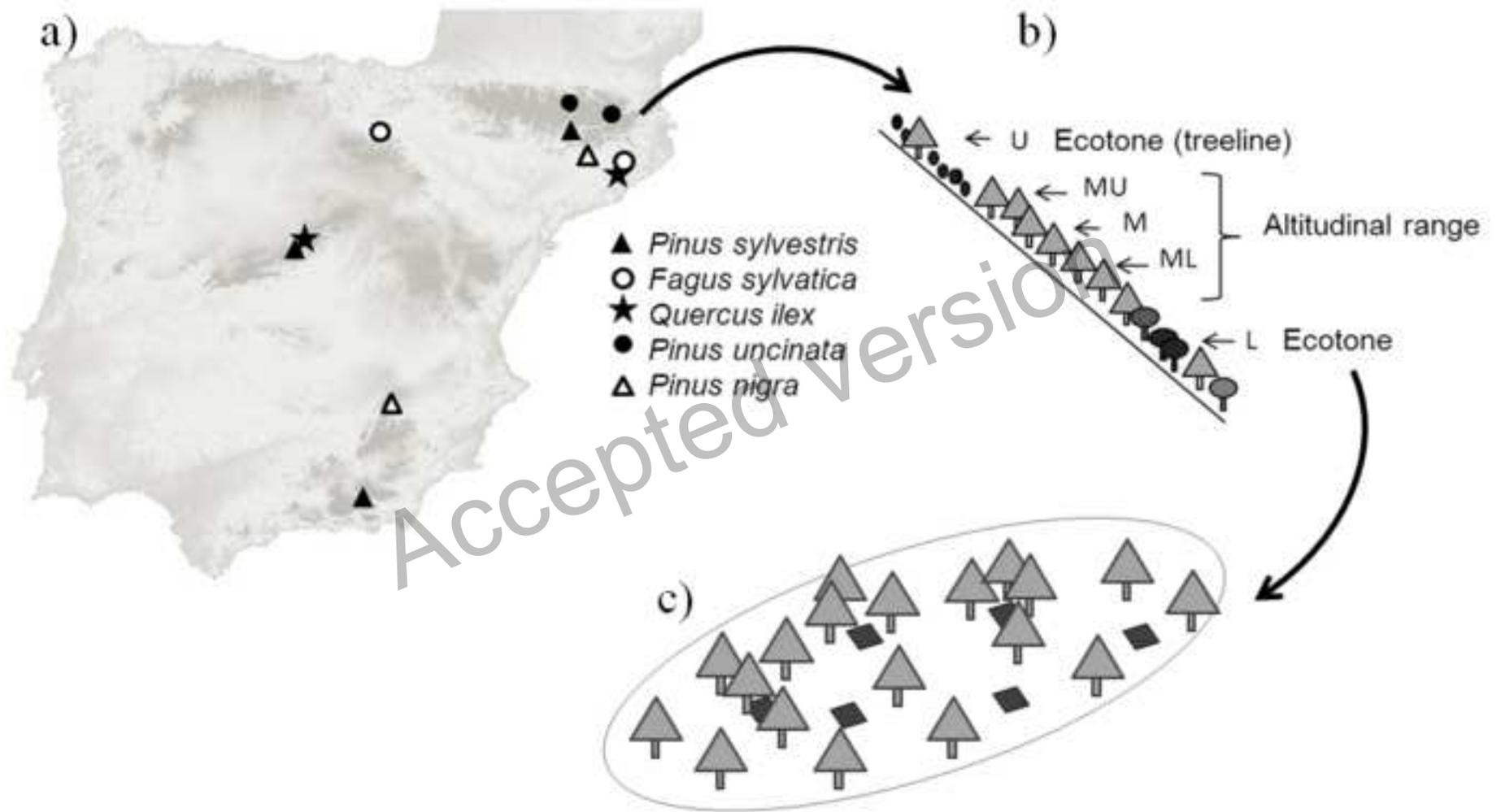


Figure2

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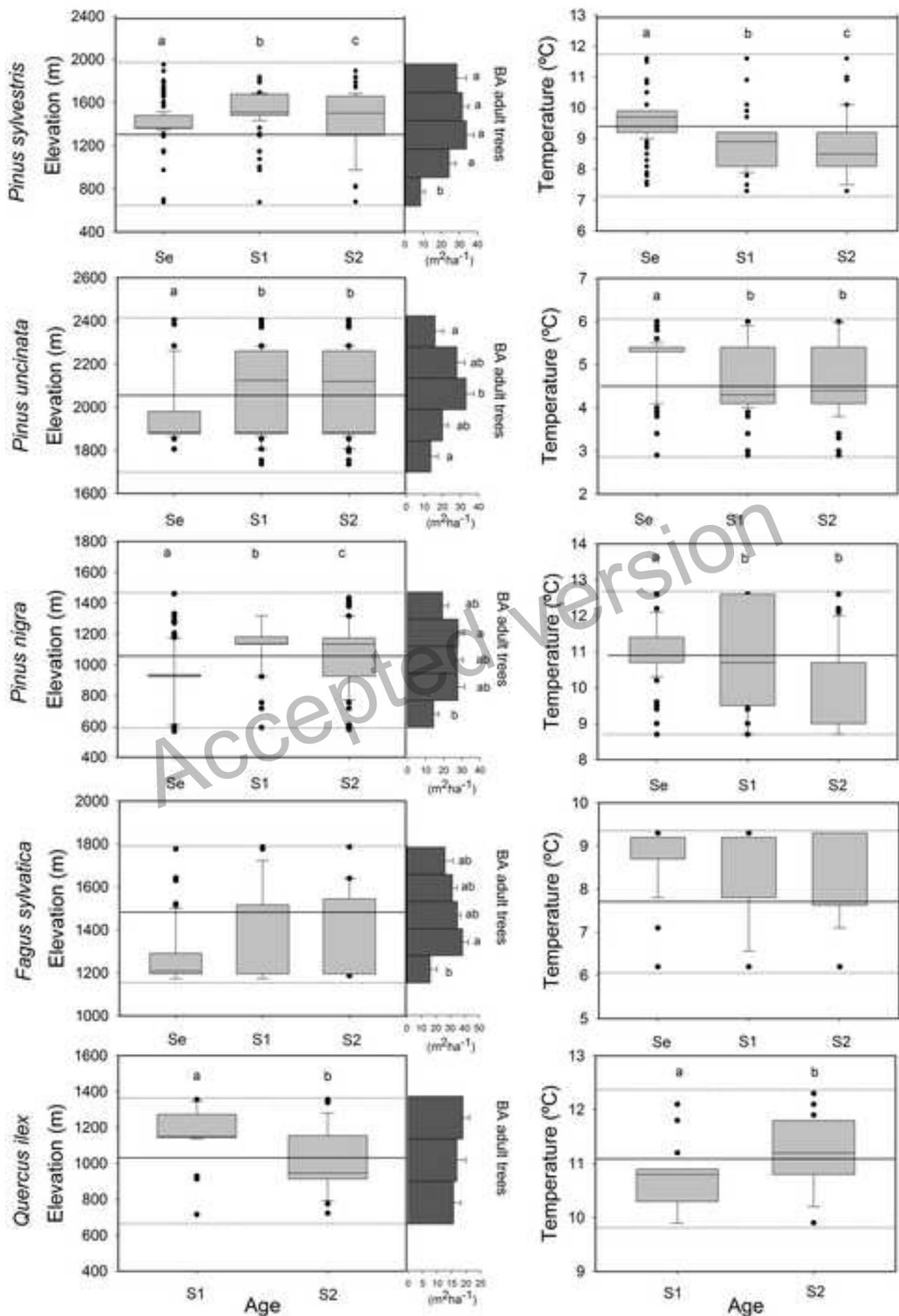


Table 1. Summary of the stabilising processes proposed by Lloret et al. (2012).

Stabilising processes	Basis	Underlying predisposing factors/ processes
Mortality mitigation	Existence of microrefugia	Site quality
		Facilitation
	Adaptation, acclimation ability	Tolerance
		Plasticity
		Phenotypic variability
Mortality compensation	Enhanced future survival or recruitment ¹	Beneficial effects of climate change
		Release competition
		Release antagonism
		Increase mutualism

¹ By improvement of the conditions for recruits or adult reproductive performance.

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Table 2. Summary of the best Generalized Linear Models (species-specific data) and Generalized Linear Mixed Model (pooled data) analysing the effect of the elevation level on the abundance of juveniles (number of individuals per plot). It is specified the sample size -number of plots surveyed- (n), the degrees of freedom (d.f.), the explanatory variable deviance (D), the probability of the chi-square tests of the variable effects ($P(\chi^2)$), AIC_{model} for the fitted model; the variation of AIC_{model} referred to the null models ($\Delta AIC = AIC_{\text{null}} - AIC_{\text{model}}$) and the explained deviance of the model (i.e. the reduction in deviance from the null to the fitted model, as a percentage of the deviance for the null model, D_{model} , expressed as a decimal). Outcomes shaded are those variables with a significant effect over the response variable in terms of deviance at $P(\chi^2) < 0.05$. For the covariates *Tree density* and *dbh* (diameter at breast height) the sign of the effect is specified in brackets after the $P(\chi^2)$, when significant.

	<i>Pinus sylvestris</i> (n=90)			<i>Pinus uncinata</i> (n=60)			<i>Pinus nigra</i> (n=60)			<i>Fagus sylvatica</i> (n=60)			<i>Quercus ilex</i> (n=36)			All species pooled (n=306)		
	d.f	D	$P(\chi^2)$	d.f	D	$P(\chi^2)$	d.f	D	$P(\chi^2)$	d.f	D	$P(\chi^2)$	d.f	D	$P(\chi^2)$	d.f	D	$P(\chi^2)$
Site	2	40.238	<0.0001	1	10.439	0.0012	1	23.430	0.0000				1	2.0446	0.0248	-	-	-
Elevation	4	28.217	<0.0001	4	21.221	0.0003	4	4.567	0.3347	4	10.001	0.0404	2	3.3223	0.0411	4	20.990	0.0003
Tree density	1	3.280	0.0701(-)				1	4.932	0.0264 (-)									
dbh										1	8.377	0.0038 (+)	1	4.0933	0.0430 (+)	1	3.840	0.0498 (+)
AIC_{model}	321.00			296.21			289.39			88.46			180.60			365.02		
ΔAIC	29.61			14.24			12.85			4.74			0.14			14.83		
D_{model}	0.64			0.43			0.43			0.53			0.26			0.07		

Table 3. Summary of the best Generalized Linear Mixed Model analysing the effect of the elevation level on the individual mean growth for each species and globally (pooled standardized data), for individuals from 1 to 5 years (S1) or individuals older than 5 years (S2). It is specified the degrees of freedom (d.f.), the explanatory variable deviance (D), the probability of the chi-square tests of the variable effects ($P(\chi^2)$), the sample size -number of individuals measured- (N), AIC_{model} for the fitted model; the variation of AIC_{model} referred to the null models ($\Delta AIC = AIC_{\text{null}} - AIC_{\text{model}}$) and the explained deviance of the model (*i.e.* reduction in deviance from the null to the fitted model, as a percentage of the deviance for the null model, D_{model} , expressed as a decimal). Outcomes shaded presented a significant effect over the response variable in terms of deviance at $P(\chi^2) < 0.05$. The sign of the effect of the covariate *BA* (basal area) appears in brackets after the $P(\chi^2)$, when significant.

		<i>Pinus sylvestris</i>			<i>Pinus uncinata</i>			<i>Pinus nigra</i>			<i>Fagus sylvatica</i>			<i>Quercus ilex</i>			All species pooled		
		d.f.	D	$P(\chi^2)$	d.f.	D	$P(\chi^2)$	d.f.	D	$P(\chi^2)$	d.f.	D	$P(\chi^2)$	d.f.	D	$P(\chi^2)$	d.f.	D	$P(\chi^2)$
S1	Elevation	4	113.518	<0.0001	4	11.877	0.0183	4	14.401	0.0061	4	6.726	0.1511	4	6.203	0.0450	4	112.455	<0.0001
	BA	1	12.304	0.0005(-)							1	1.545	0.2139				1	5.389	0.0203 (-)
	N	838			252			195			64			109			1458		
	AIC_{model}	1014.88			205.92			522.21			224.77			156.27			-169.2678		
	ΔAIC	115.82			3.88			14.71			-1.73			2.20			107.84		
D_{model}	0.11			0.06			0.06			0.04			0.04			1.7			
S2	Elevation	4	17.425	0.0016	4	17.695	0.0014	4	11.532	<0.0001	4	6.238	0.1821	4	0.713	0.7001	4	9.758	0.0447
	BA	1	8.586	0.0034(-)	1	8.825	0.0030 (-)				1	0.808	0.3687	1	3.264	0.0708(-)	1	18.137	<0.0001(-)
	N	211			332			292			26			124			985		
	AIC_{model}	258.79			594.17			295.21			73.46			162.75			303.9562		
	ΔAIC	16.01			16.52			17.37			-2.95			-2.02			17.90		
D_{model}	0.1			0.04			0.08			0.11			0.03			0.09			

Accepted version