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1 **How neighbourhood interactions control the temporal stability and**
2 **resilience to drought of trees in mountain forests.**

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15

16 **ABSTRACT**

- 17 1. Over the coming decades, the predicted increase in frequency and intensity of extreme events such
18 as droughts is likely to have a strong effect on forest functioning. Recent studies have shown that
19 species mixing may buffer the temporal variability of productivity. However, most studies have
20 focused on temporal stability of productivity, while species mixing may also affect forest
21 resilience to extreme events. Our understanding of mechanisms underlying species mixing effects
22 on forest stability and resilience remains limited because we ignore how changes from
23 intraspecific to interspecific interactions in the neighbourhood of a given tree might affect its
24 stability and resilience to extreme drought (i.e. response during and after this drought). This is
25 crucial to better understand forests' response to climate change and how diversity may help
26 maintain forest functioning.
- 27 2. Here we analyzed how local intra- or interspecific interactions may affect the temporal stability
28 and resilience to drought of individual trees in French mountain forests, using basal area
29 increment data over the previous 20 years for *Fagus sylvatica*, *Abies alba*, and *Quercus*
30 *pubescens*. We analyzed the effect of interspecific competition on i) the temporal stability and ii)
31 the resilience to drought (resistance and recovery) of individual tree radial growth.
- 32 3. We found no significant interspecific competition effect on temporal stability, but species-specific
33 effects on tree growth resilience to drought. There was a positive effect of heterospecific
34 proportion on the drought resilience of *Q. pubescens*, a negative effect for *A. alba*, and no effect
35 for *F. sylvatica*. These differences may be related to interspecific differences in water use or
36 rooting depth.
- 37 4. *Synthesis*: In this study, we showed that stand composition influences individual tree growth
38 resilience to drought, but this effect varied depending on the species and its physiological
39 responses. Our study also highlighted that a lack of biodiversity effect on long-term stability

40 might hide important effects on short-term resilience to extreme climatic events. This may have
41 important implications in the face of climate change.

42 **Key words:** Diversity, mountain forest, drought resistance and recovery, climate change, growth

43 INTRODUCTION

44 In the last decades, on-going climate change has led to a sharp rise in temperatures
45 (Intergovernmental Panel on Climate Change, 2014), as well as an increase in the frequency of extreme
46 events, especially droughts, in southern Europe, for temperate and Mediterranean ecosystems (Pachauri et
47 al., 2014). In these ecosystems, severe drought events have already significantly disrupted terrestrial
48 ecosystem functioning (Allen et al., 2010; Sterl et al., 2008) and coping with their increase in intensity and
49 frequency will certainly be a key challenge in the near future (Seidl, Schelhaas, Rammer, & Verkerk,
50 2014).

51 As a result, many studies have focused on testing whether biodiversity could buffer changes in
52 ecosystem functioning caused by climate variability and extremes events. These biodiversity effects were
53 first evaluated using theoretical models (Yachi & Loreau, 1999), then tested using field experiments in
54 grassland ecosystems (Tilman, Reich, & Knops, 2006). In forests, the relationship between diversity and
55 stability has mostly been evaluated in observational studies (DeClerck, Barbour, & Sawyer, 2006;
56 Charlotte Grossiord, Granier, Gessler, Jucker, & Bonal, 2014; Jucker, Bouriaud, Avacaritei, & Coomes,
57 2014). Most studies have found evidence for a positive effect of species diversity on the temporal stability
58 of ecosystem functioning (DeClerck et al., 2006; Jucker et al., 2014), but large uncertainty remains on
59 how this diversity effect varies according to climate. Several mechanisms have been put forward to
60 explain why biodiversity could increase forest ecosystems temporal stability. Firstly, species diversity
61 might lead to an increase in average productivity because of complementarity between species, a process
62 calledoveryielding (Loreau, 2001). For example, resource acquisition strategies could vary from one
63 species to another, because of differences in rooting depth that could affect access to water and nutrients
64 (Bréda, Huc, Granier, & Dreyer, 2006), differences in crown shape that could affect light interception, or
65 differences in phenology that could affect resources partitioning over time (Jucker et al., 2014; Pretzsch &
66 Schütze, 2016). Thisoveryielding effect is supposed to positively affect temporal stability (Loreau & de
67 Mazancourt, 2013). These effects are not necessarily symmetrical between species and can be more

68 beneficial for the most competitive species in a mixture (Chen et al., 2016; Toïgo et al., 2015). Secondly,
69 differences between species response to temporal variation in climatic or biotic (e.g. pathogens) conditions
70 can result in temporal asynchrony in their growth, which has been shown to be a strong stabilizing factor
71 at the stand scale (Drobyshev, Gewehr, Berninger, & Bergeron, 2013; Pretzsch, Schütze, & Uhl, 2013;
72 Rozas, Lamas, & García-González, 2009).

73 Besides temporal stability, *i.e.* a metric measuring long-term patterns, tree resilience to extreme
74 events will also be crucial in the face of climate change. It is thus essential to also explore the effect of
75 biodiversity on tree resilience if we are to gain a comprehensive understanding. Several definitions of
76 ecosystems resilience exist in the literature (see Ingrisch & Bahn, 2018), but most of them share the idea
77 that *resilience* can be divided into *resistance* and *recovery* (see Fig.1A for our study). Resistance is related
78 to the immediate reduction in performance during an extreme event and recovery is the ability to recover
79 after it (Lloret, Keeling, and Sala 2011). The role of diversity on ecosystem resilience to extreme climate
80 events, like drought, has been less studied than the role of diversity on temporal stability (Donohue et al.,
81 2016). There is no consensus about diversity effects on resilience to drought in forest ecosystems: some
82 studies have shown positive effects (Lebourgeois, Gomez, Pinto, & Mérian, 2013; Gazol & Camarero
83 2016), other studies found species- or site-specific effects (Grossiord et al., 2014; Jourdan, Lebourgeois,
84 & Morin, 2019; Merlin, Perot, Perret, Korboulewsky, & Vallet, 2015; Mölder & Leuschner, 2014;
85 Pretzsch et al., 2013), or no effects (DeClerck et al., 2006; Forrester et al., 2016). In addition, our
86 understanding of the underlying mechanisms of the biodiversity effect on resilience is still limited,
87 although they are likely to be like those invoked for temporal stability, as mentioned above.

88 Studies focusing on diversity effects on temporal stability or resistance and recovery to extreme
89 events have been mainly carried-out at the stand scale, *i.e.* considering the whole community (DeClerck et
90 al., 2006; del Río et al., 2017; Hutchison, Gravel, Guichard, & Potvin, 2018; Jourdan et al., 2019; Merlin
91 et al., 2015). Yet, if we aim at understanding the role of interspecific interactions in promoting diversity
92 effects on temporal stability and resilience, we need to focus on the local scale at which individual trees
93 interact with their neighbours. Very few studies have tackled the question of biodiversity effect on

94 stability at the local scale: some explored temporal stability (Aussenac et al., 2017), some explored
95 buffering against climate variability (Aussenac, Bergeron, Gravel, & Drobyshev, 2019) and some
96 explored resilience to extreme droughts (Gazol & Camarero, 2016; Mölder & Leuschner, 2014). To our
97 knowledge, no previous studies have evaluated temporal stability, resistance, and resilience
98 simultaneously at the individual tree level. Because of the limited number of studies at local scale, we
99 have a limited understanding of how stabilizing effects from local interspecific interactions vary between
100 species, between sites, and between mid- to long-term stability metrics and short-term drought resilience
101 metrics. Improving our understanding of these local interspecific interactions effects is, however, crucial
102 to better understand forests' response to climate change and how diversity may buffer these changes.

103 To tackle this problem, we tested whether the proportion of heterospecific trees in the
104 neighbourhood affects temporal stability and resilience to drought of individual tree growth. To do so, we
105 focused on two widespread species-mixtures in the French Alps: common beech (*Fagus sylvatica*) -
106 pubescent oak (*Quercus pubescens*) and beech - silver fir (*Abies alba*). We used a triplet-based approach
107 by sampling two monospecific stands and one mixed stand distributed across a latitudinal gradient in the
108 Alps, covering a wide range of abiotic conditions. These species are particularly interesting because they
109 differ in their physiological preferences. The first species, common beech, is generally sensitive to dry
110 conditions, despite recent reporting of higher resistance to drought (Gazol et al., 2018), and recovery from
111 drought events under specific conditions (Durrant, de Rigo, & Caudullo, 2016; Lebourgeois, Bréda,
112 Ulrich, & Granier, 2005). The second species, silver fir, grows rapidly in humid conditions (Lebourgeois,
113 Rathgeber, & Ulrich, 2010; Mauri, de Rigo, & Caudullo, 2016). Although it is relatively tolerant to
114 drought for an alpine coniferous tree and classified as a thermophilic species (Rameau, Mansion, & Dumé,
115 1999), it is less drought-tolerant than beech (Choat et al., 2012; Niinemets & Valladares, 2006), especially
116 at the edge of its range. The last species, pubescent oak, is the most drought-resistant species among the
117 three studied (Pasta et al., 2016). For each individual tree, we reconstructed time series of basal area
118 growth (a proxy of wood production), and we extracted time-series of drought stress indicators from
119 climate data. We hypothesized that increasing the proportion of heterospecific trees in the neighbourhood

120 of a given tree should promote either its temporal stability or its drought resilience. More specifically, we
121 aimed at testing the following hypotheses:

122 1) The proportion of heterospecific trees in the neighbourhood increases the temporal stability of tree
123 growth in beech-fir and beech-oak forests. This stabilizing effect can result either from the fact
124 that heterospecific proportion may increase the mean of tree growth or decrease the variance of
125 tree growth.

126 2) The proportion of heterospecific trees in the neighbourhood buffers the effect of extreme drought
127 events on tree growth. This buffering effect can result from an increase in the individual resistance
128 to drought (drought impact on the current year) or from an increase in the individual recovery rate
129 (decline of the impact of drought in the few years after). We suppose that the biodiversity effect
130 on drought resilience should vary between species depending on their physiological strategies of
131 water use.

132

133 **MATERIALS AND METHODS**

134 **Field data**

135 Our analysis relies on individual growth time-series of trees sampled in forest plots dominated by
136 one species (*i.e.* monospecific stands) or by a mixture of two species. This sampling strategy allows us to
137 study a wide range of proportions of heterospecific trees in the neighbourhood. We selected sites along a
138 latitudinal gradient from the North to the South of the French Alps (Jourdan et al., 2019). These sites are
139 (from North to South): Bauges (Combe d'Ire), Vercors (Lente), Mont Ventoux (Beaumont du Ventoux),
140 Luberon-Lagarde (Lagarde d'Apt), Grand Luberon (Saint-Martin du Castillon) and Sainte-Baume (Fig. 1).
141 Within each site we selected plots along elevation gradients with at least two elevations per site (Table
142 S1). To limit confounding factors, all plots were selected on limestone bedrock, with an aspect from North
143 to West.

144 Plots were determined as monospecific ones when at least 90% of the total basal area of the plot
145 was represented by a single target species, while mixed plots were dominated by a mixture of two species,
146 with the relative basal area of each species representing at least 40% of the total basal area of the plot. The
147 other species growing on the plots (*Acer pseudoplatanus*, *Sorbus aucuparia*, *Ilex aquifolium*) were not
148 considered because they represent a negligible part of total basal area. Beech was present over the entire
149 latitudinal gradient but was mixed with silver fir in the North (Bauges, Vercors, Mont Ventoux) and
150 downy oak in the South (Luberon Lagarde, Grand Luberon, Sainte-Baume). For most sites, the stand
151 structure was high forest, except in Grand Luberon where most stands were coppice forests. These forests
152 have been managed for many decades (except in Sainte Baume and Grand Luberon), but we selected plots
153 without management during the last decades to limit direct silvicultural effects (following local forest
154 managers' advice). To the extent possible, the plots have been grouped in triplets inside a site, *i.e.* the
155 combination of a beech monospecific plot, a fir or oak monospecific plot, and one mixed plot (fir-beech or
156 oak-beech). Forest structure and total basal area were homogenous among the three plots of each triplet,
157 and plots inside a triplet were as close together as possible (177 m apart on average, and at a similar
158 elevation) to minimize topographic and micro-climatic differences. In total, 67 plots within 22 triplets
159 were sampled between 2013 and 2016 (Table S1), gathered in 22 triplets.

160 A plot was delimited by a 17.5m-radius circle, including a central area of 10m-radius and 7.5m
161 buffer zone (Fig. 1). In the central area, we measured several tree characteristics (species identity,
162 localization based on azimuth and distance, height, and diameter at breast height [DBH]), and we sampled
163 one core by tree at breast height for dendrochronological analyses using a Pressler borer. All trees with a
164 DBH > 7.5 cm were cored, except for coppice stands in which only the largest stem of each coppice was
165 cored. In the buffer area, only dominant trees were measured (but not cored) to consider their competitive
166 impact. Dominant trees were identified as the trees with a DBH larger than the median DBH of trees in the
167 central area. In this analysis, we decided to consider only dominant trees because they represented most of
168 the readable cores, with their interannual patterns being more visible. Moreover, we considered that, as
169 dominant trees, they exerted most of the competitive effects.

170 To precisely describe the neighbourhood of each tree, we mapped all trees in the plots. For each
171 tree in the central area, we described its neighbourhood. We selected the most relevant indices to describe
172 the dual effect of local neighbours on the target tree (i.e. local competition and proportion of
173 heterospecific trees in the neighbourhood) based on AIC (Akaike Information Criterion) comparison
174 (Table S2). We tested four pair of indices. First, we tested g_{hete} and BA , with BA being the total basal area
175 of all dominant trees in neighbourhood (i.e. trees with a DBH superior to mean DBH of each plot in a 7 m
176 radius), and g_{hete} being the basal area proportion of heterospecific trees in this neighbourhood. Then we
177 explored other indices to describe the heterospecific competition in the neighbourhood: BA_{hete} and
178 BA_{consp} , with BA_{consp} the basal area of conspecific trees and BA_{hete} basal area of heterospecific trees; d_{hete}
179 and D , with D the density of dominant trees and d_{hete} the percentage of heterospecific trees; and D_{hete}
180 and D_{consp} , with D_{consp} the density of conspecific trees and D_{hete} density of heterospecific trees.
181 According to the AIC comparison, the best pair of indices is g_{hete} and BA_{tot} .

182 We chose to compute competition indices with a 7m radius because this captured the most
183 important competitors and allowed to use all trees in the central area. Comparison of these indices with
184 competition indices computed in larger area (radius of 10, 12.5, 15 m), showed a correlation
185 (quantification via linear model – with one model per site -, all species together) close to 1 and with r^2
186 often higher than 0.75 for our dataset (see Table S3).

187

188 **Dendrochronological data**

189 We measured tree rings for 17 years before sampling, i.e. from 1995 to 2012. An image of each
190 tree ring was first acquired with a large-resolution camera coupled with a binocular lens. The width of
191 each ring was then assessed with ImageJ software (<https://imagej.nih.gov/ij/index.html>), with an accuracy
192 of 0.01 mm. All cores were cross-dated identifying pointer years (with 80% higher or lower growth than
193 mean increment, see Lebourgeois & Merian, 2012). Diameter increments were transformed in basal area

194 increment (*BAI*) using reconstructed DBH (Biondi & Qeadan, 2008; Kershaw, Ducey, Beers, & Husch,
195 2016). In total we obtained growth time-series for 840 trees, with 253 beeches in North, 188 beeches in
196 South, 221 firs and 178 oaks.

197 **Temporal stability**

198 *Productivity, variance and temporal stability*

199 We used the annual tree basal area increment (*BAI*) for the 1995-2012 period to evaluate the
200 individual Temporal Stability (*TS*), defined as the inverse of the coefficient of variation of basal area
201 increment time-series (Lehman & Tilman, 2000):

$$202 \quad TS = \frac{\mu_{BAI}}{\sigma_{BAI}} \quad (1)$$

203 with μ_{BAI} and σ_{BAI} being respectively the mean and standard deviation of individual tree basal area
204 increment time-series between 1995 and 2012. We also studied μ_{BAI} and σ_{BAI} separately to understand
205 which component of *TS* was the most sensitive.

206 *Statistical model*

207 We analysed *TS*, μ_{BAI} and σ_{BAI} with the following model:

$$208 \quad Y_i = a_s + c_1 * DBH_i + c_2 * BA_i + c_3 * g_{hete,i} + b_t + e_i \quad (2)$$

209 where *i* is the tree index, *Y_i* is *TS*, $\log(\mu_{BAI})$ or $\log(\sigma_{BAI})$. *DBH_i* is the diameter at breast height, *BA_i* is
210 the basal area in the neighbourhood of tree *i* (*i.e.* at a maximum distance of 7 m of tree *i*), *g_{hete}* is the
211 proportion of the basal area of heterospecific trees in neighbourhood of the focal tree *i*. *a_s* is a fixed site
212 effect (Bauges, Vercors, Ventoux, Grand Luberon, Luberon Lagarde or Sainte-Baume), *c₁₋₃* are the
213 respective fitted coefficients, *b_t* is a triplet *t* random effect, and *e_i* is the residual normal error. According to
214 hypothesis 1), *c₃* is expected to be significantly positive for *TS* model. We fitted a model separately for
215 each species and region in the Alps (*i.e.* beech in the North, beech in the South, fir in the North and oak in
216 the South). We used $\log(\mu_{BAI})$ and $\log(\sigma_{BAI})$ because these transformations allowed to normalize μ_{BAI}
217 and σ_{BAI} . Analyses were carried out with the *lme* function of package *nlme* in the R software (R version
218 3.3.0).

219 **Resistance and recovery**

220 *Climate data*

221 We used the Standardized Precipitation Evapotranspiration Index (*SPEI*) to determine the onset,
222 duration and magnitude of drought events with respect to normal conditions. *SPEI* is derived of the *SPI*
223 (Standardized Precipitation Index, Guttman, (1999)), and represents a simple climatic water balance
224 (Thornthwaite, 1948) calculated at different time scales, using the monthly (or weekly) difference between
225 precipitation and potential evapotranspiration (Vicente-Serrano, Beguería and López-Moreno 2010;
226 Vicente-Serrano et al. 2013). *SPEI* is frequently used in ecological studies using radial growth data
227 (Hutchison et al., 2018; Merlin et al., 2015; Pretzsch et al., 2016).

228 We calculated *SPEI* from February to July - hereafter identified as *SPEI*₀₇ (Vanoni, Bugmann,
229 Nötzli, & Bigler, 2016) - between 1995 and 2012 with R package *SPEI* (Vicente-Serrano, Beguería and
230 López-Moreno 2010). *SPEI* was computed from 1 km-resolution maps of precipitations and potential
231 evapotranspiration, interpolated from weather station data (Piedallu & Gégout, 2007; Piedallu, Gégout,
232 Lebourgeois, & Seynave, 2016). The *SPEI* time-series by site are presented in Fig. S4. The threshold at
233 which *SPEI* corresponds to a year with a drought affecting significantly the vegetation growth is likely to
234 vary between species and sites. Nevertheless, for the sake of simplicity, we used a unique threshold in our
235 analysis. An AIC comparison (exploring value between -0.5 and -1.5 with a 0.02 step, not shown here)
236 showed that for our dataset the best threshold was -1.17. This value is in agreement with a recent
237 experimental study in grasslands that used a threshold of -1.28 (Isbell et al., 2015) and a global study
238 based on remote sensing data that used a threshold of -1 (Schwalm et al., 2017).

239 We chose to use *SPEI* calculated from February to July, because this period is crucial to refill the
240 soil profile to field capacity of forest plots (February-March) and corresponds to the main part of the
241 growth season in these sites (April-July). Autumn and winter months (October-January) seems less crucial
242 to appreciate drought stress on forest. We used also *SPEI* from April to September to quantify drought
243 stress, and the results were similar.

244 *Statistical model*

245 While other studies have compared tree growth before and after a stressful event (Lloret et al.,
246 2011; Pretzsch et al., 2013; Trouvé, Bontemps, Collet, Seynave, & Lebourgeois, 2017; Zang, Hartl-Meier,
247 Dittmar, Rothe, & Menzel, 2014), we chose to use a distributed lag effect model of $SPEI_{07}$ to estimate tree
248 resilience to drought (Gasparrini, 2011). We included a linear lag effect of SPEI in a linear model of
249 individual tree growth that controls for additional covariates. More precisely, we modelled the annual
250 basal area increment ($\log BAI$, BAI log-transformed to account for the skewed distribution) as function of
251 tree size (DBH), local competitive environment (BA and g_{hete}), and distributed lag effect of $SPEI$ and their
252 interaction with local proportion of heterospecific trees in the neighbourhood.

253 We modelled the drought lag effect from the current year (lag0) up to four previous years (*i.e.*
254 lag1, lag2, lag3 and lag4) with distributed lag effects based on i) a threshold function below -1.17 $SPEI$
255 and ii) a linear function to represent the temporal lag effect of drought on tree growth. The threshold
256 function corresponds to a transformation of $SPEI$ into a new variable $SPEI_t$ such as $SPEI_t = 0$ if $SPEI \geq -$
257 1.17 and $SPEI_t = -1.17 - SPEI$, if $SPEI < -1.17$. $SPEI_t$ is a positive and increasing function drought stress
258 intensity (whereas drought stress corresponds to negative value of $SPEI$). The temporal distributed lag
259 effect was modelled using a linear model with an intercept (see Gasparrini, 2011 for more details on
260 distributed lag effect models). This linear trend was supported by a preliminary analysis assuming
261 unconstrained lag effects. A distributed lag effect allows us to represent the delayed effect of a variable (in
262 our case $SPEI_t$) as the sum of the effect until a specific number of lag years is reached (4 in our case). The
263 equation 3 shows the lag effect for a given year y :

264
$$\sum_{l=0}^4 \beta_l SPEI_{t-y-l}$$

265 A linear lag effect model is fitted by constraining the β coefficients as $\beta_l = a + b * l$, where l is
266 the lag year (l in 0 to 4). Our distributed lag effect model is closely similar to the classical representation
267 of resilience in term of resistance and recovery (see Fig. S5 and Lloret et al., 2011) with the intercept at
268 lag0 (parameter a) representing the immediate growth reduction due to drought and the linear recovery

269 over time (parameter b) determining the recovery rate after stress. The parameters a and b can be
 270 estimated by recasting as:

$$271 \quad \sum_{l=0}^4 \beta_l SPEIt_{y-l} = a * \sum_{l=0}^4 SPEIt_{y-l} + b * \sum_{l=0}^4 l * SPEIt_{y-l}$$

$$272 \quad = a * lag_{intercept}(SPEI_y) + b * lag_{slope}(SPEI_y), (3)$$

273 with $lag_{intercept}(SPEI_y) = \sum_{l=0}^4 SPEIt_{y-l}$ and $lag_{slope}(SPEI_y) = \sum_{l=0}^4 l * SPEIt_{y-l}$.

274 The full fitted model is given by the following equation:

$$275 \quad \log BAI_{s,t,i,y} = c_{0,s} + c_1 * DBH_i + c_2 * BA_i + c_3 * g_{hete,i} + a * lag_{intercept}(SPEI_y) + b * lag_{slope}(SPEI_y) +$$

$$276 \quad a_{gh} * lag_{intercept}(SPEI_y) * g_{hete,i} + b_{gh} * lag_{slope}(SPEI_y) * g_{hete,i} + d_t + d_{i,t} + e_{i,t,y} \quad (4)$$

277 where i , t , and y are respectively the tree index, the triplet and the year. $c_{0,s}$ is site dependent intercept (s
 278 corresponding to one of the six different sites). DBH_i is the diameter at breast height, BA_i is the total basal
 279 area of dominant trees in the neighbourhood, $g_{hete,i}$ is the ratio between heterospecific trees basal area and
 280 total trees basal area in the neighbourhood of tree i and c_{1-3} are the respective fitted coefficients. d_t and $d_{i,t}$
 281 are respectively the triplet and individual nested in triplet random effect and $e_{i,t,y}$ is the residual normal
 282 error. a and b represent respectively the immediate growth reduction due to drought (resistance) and the
 283 linear recovery over time (recovery). The parameters a_{gh} and b_{gh} represent the interaction between the
 284 proportion of heterospecific trees in the neighbourhood ($g_{hete,i}$) and resistance or recovery respectively.
 285 This interaction allows to test how local mixing may influence resistance to and recovery from drought.
 286 According to hypothesis 2, we expected a_{gh} and b_{gh} to be significantly positive. This model was fitted
 287 separately per species - beech, fir and oak - and region - North (for Bauges, Vercors, Ventoux) and South
 288 (for Luberon Lagarde, Grand Luberon and Sainte-Baume) - with *lme* of package *nlme* and package
 289 DLNM with R software (R version 3.3.0). The methods used are illustrated in Fig. S5 for the sake of
 290 clarity.

291

292 **RESULTS**

293 **Temporal stability**

294 We did not find any effect of the proportion of heterospecific trees in the neighbourhood on the
295 long-term temporal stability of tree growth, or on its components taken separately (Fig. 2 and Tables S6,
296 S7, S8). For beech in the south, the effect of the proportion of heterospecific trees was weakly negative.
297 We also did not find any effect of the total basal area of competitors in the neighbourhood on tree growth,
298 irrespective of species. Only tree DBH significantly affected mean individual tree growth and its standard
299 deviation but it did not significantly affect temporal stability. In fact, there was a significant positive
300 correlation between the mean and the standard deviation of the individual productivity, for each species
301 considered separately ($P < 0.0005$ and $r^2 > 0.8$, see Table S9).

302 **Resistance and recovery to drought**

303 *Drought effect on growth*

304 We found a significant effect of drought (assessed by SPEI) considering a lag of up to four years
305 for the three species in all regions (Table 1). Resistance to and recovery from drought (measured by
306 intercept and slope of the distributed lag effects) varied among species and regions (Table 1). The
307 resistance and recovery to drought of fir was lower than beech in the North, consistently with its lower
308 physiological tolerance to drought. Also consistently with the greater drought tolerance of oak compared
309 to beech, we found that the resistance was slightly lower for beech compared to oak in the South. In
310 addition, there was a lower resistance but a greater recovery of beech trees in the South than beech trees in
311 the North (Fig 3).

312 *Effect of the proportion of heterospecific trees on resistance and recovery*

313 We found a significant effect of the proportion of heterospecific trees (in terms of basal area) on
314 individual drought resistance for oak in the South and for fir in the North, but not for beech (Table 1 and
315 Fig. 3). Heterospecific competitors thus significantly increased the resistance of oaks but decreased the
316 resistance of firs.

317 The effect of the proportion of heterospecific trees on individual recovery after drought was weak.
318 The trend was significant only for fir (Table 1 and Fig. 3), showing a faster recovery with a larger

319 proportion of heterospecific trees in the neighbourhood. The other models considering different pairs of
320 indices to quantify local competition and proportion of heterospecific trees in the neighbourhood yielded
321 similar results.

322 *Direct effect of heterospecific trees proportion on tree growth*

323 The overall effect of the proportion of heterospecific neighbours on tree BAI varied depending on
324 species. It was not significant for oak, fir, and beech in the North, while it was significantly negative for
325 beech in mixed plots with oak in the South.

326 **DISCUSSION**

327 We found that the local proportion of heterospecific trees did not affect the individual long-term
328 temporal stability of growth of individual trees but it had a significant effect on tree resistance to and
329 recovery from severe drought, as assessed over 4 years after the event. For all species, severe drought had
330 a significant negative effect on individual tree growth followed by a progressive recovery. The
331 significance and the direction of the effect of the local proportion of heterospecific trees on drought
332 resilience was different between species and seemed related to their drought tolerance.

333 **Temporal stability of individual trees independent of stand composition**

334 There was no effect of the proportion of heterospecific trees on the temporal stability of tree
335 productivity for the three studied species (Table 1). We are unaware of any studies that have quantified
336 temporal stability in growth of any of the species in our study, even at a stand level. However there were a
337 few studies of how their mean productivity responded to species mixing, which allowed to carry-out some
338 comparisons with our results. The mean productivity of beech increases in mixed stands with silver fir
339 (Toïgo et al., 2015), possibly because mixed stands diminish strong intraspecific competition in beech
340 (Bolte, Kampf, & Hilbrig, 2013). However, we found no evidence of this in the growth of individual
341 beech trees (Fig. 2). Moreover, mean growth of silver fir trees was not affected in mixed stands with beech
342 compared with monocultures, which is consistent with Toïgo et al. (2015). In agreement with our results,

343 Toigo et al. (2015) also found that the degree of mixture only weakly affected the stand productivity of
344 beech (positively) and oak (negatively) in beech-oak mixed stands. In this case, the comparison between
345 their results and ours is, however, limited because the oak species studied are not the same: sessile oak
346 (*Quercus petraea* Liebl.) instead of pubescent oak.

347 We also expected that the temporal standard deviation of individual growth could vary with the
348 proportion of heterospecific trees in the neighbourhood, especially considering our results on resistance
349 and recovery. Furthermore, it has been shown that mixing species can have a stabilizing effect on the
350 productivity because mixed stands may decrease either the temporal standard deviation within species
351 (Aussenac et al., 2019 at individual level or del Río, Condés, & Pretzsch, 2014 at stand level) or the
352 covariance between species (Aussenac et al., 2017 at individual level or Jucker et al., 2014 at stand level).
353 We did not find such a stabilizing effect on the temporal standard deviation within species for any of the
354 three species studied (see Table S8). Because our study was focusing on a heterospecific interaction effect,
355 we did not explore the effect on covariance.

356 The impact of climate conditions on the strength of the diversity-stability in productivity
357 relationships remains largely unknown, especially in tree communities. To our knowledge, only Jucker et
358 al. (2014) and del Río et al. (2017) explored this effect and found that environmental conditions may
359 affect the stability of aboveground wood production only at community level. Yet, depicting how climate
360 conditions may impact diversity effect on forest functioning appears critical in the context of on-going
361 climate change that could deeply impact forest structure for centuries, as shown through past climatic
362 events (see Pederson et al., 2014). Mediterranean and/or mountainous environments are particularly
363 sensitive to future environmental changes (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005).
364 Furthermore, differences between the responses of species are supposed to be more marked in stressful
365 conditions, according the stress gradient hypothesis (*SGH*, Lortie and Callaway 2006; Maestre et al.
366 2009), thus exacerbating the diversity effect in such conditions as confirmed through simulations (Morin
367 et al., 2018).

368 **The effect of heterospecific interactions on tree resilience to drought depends**
369 **on species physiological differences**

370 Pubescent oak benefits from being in mixed stands with beech because of the small, but
371 significant, positive effect on its resistance to drought. This may be explained by a reduced competition
372 for water acquisition in mixed stands compared with monocultures for oak (Cavin, Mountford, Peterken,
373 & Jump, 2013; Schwendenmann, Pendall, Sanchez-Bragado, Kunert, & Hölscher, 2015). In fact, beech
374 trees are less drought-resistant than oak trees (drought resistance indices are respectively 2.4 ± 0.43 against
375 4.1 ± 0.25 according to Niinemets & Valladares, (2006)), and oaks may thus experience a water
376 competition release during a drought event when mixed with beeches, which is consistent with the
377 statistically significant positive interaction between resistance and heterospecific proportion in the
378 neighbourhood that we found (Fig. 3 –lower-left panel). As there is no previous study focusing on
379 pubescent oak, we compared our results with studies on mixed sessile oak and Scots pine stands (Merlin et
380 al., 2015) at an individual level. Merlin et al. (2015) suggested that stand composition had no effect on
381 resilience or resistance for both species. This study was, however, conducted in sites that were less
382 drought-stressed than in our study. Individual beech tree growth can be less drought-sensitive when mixed
383 with some other tree species (*Acer pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *Tilia platyphyllos*),
384 but not when mixed with oak species (*Q. petraea*, *Quercus robur*) (Mölder & Leuschner 2014). These
385 findings on beech-oak mixing effect seems to corroborate our own results: replacing beeches by oaks in
386 the neighbourhood of a beech tree had no negative effect on the resilience (resistance and recovery) to
387 drought of the beech tree. However, in contrast to our study, Pretzsch et al. (2013) found a positive mixing
388 effect on the resilience of beech growth to droughts at a stand level in beech-oak (*Q. petraea*) forests
389 compared with beech in monocultures.

390 In beech-fir stands, the resistance of beech trees was independent of the local proportion of
391 heterospecific trees. In contrast, firs are negatively affected by an increasing proportion of beeches in their
392 neighbourhood during extreme drought events. This finding is in agreement with the fact that beech trees

393 are more drought-tolerant than fir, as shown by Niinemets & Valladares, (2006) (drought resistance
394 indices are respectively 2.4 ± 0.43 against 1.81 ± 0.28) and by Choat et al. (2012) (ψ_{88} safety margin,
395 defined as the water potential at which 88% conductivity is lost, are respectively 1.43 against 0.40), thus
396 relying on two different assessment of drought tolerance. In this kind of mixed stands, the competition
397 between beech and fir trees could be stronger than the competition between firs. Surprisingly, studies
398 exploring the relationship between diversity and fir sensitivity to drought have shown a positive effect of
399 increasing diversity of the nearby composition (Gazol & Camarero, 2016, with fir-beech-Scots pine stands
400 and Lebourgeois et al., 2013, with fir-beech-spruce stands). This is in contradiction with our results on
401 resistance but agree with our results on recovery rate after drought, as we found that recovery of fir trees
402 increased with the proportion of beeches in their neighbourhood. This could be explained by differences in
403 the phenological niches of fir and beech. Indeed, the growth season of an evergreen species like fir starts
404 earlier than the one of a deciduous species like beech. Thus, fir trees start to uptake resources (light
405 obviously, but also water and nutrients) earlier than beech trees. This could give an advantage to fir trees
406 competing with beech trees by recovering faster after a drought event than fir trees in monospecific stands.
407 However, we did not find any effect of mixed species on fir growth, contrary to Gazol & Camarero (2016)
408 and Lebourgeois et al. (2013), who found a positive effect of the heterospecific proportion in the stand.
409 Differences in site conditions could explain differences in the observed patterns between our results and
410 previous studies. Mixing effects may be more pronounced in sites experiencing greater drought stress than
411 occurring in our sites (according to the stress gradient hypothesis; Lortie and Callaway 2006; Maestre et
412 al. 2009), which may accentuate diversity effects in those sites.

413 These different results showed that in a mixed stand, the physiological differences between the co-
414 existing species may strongly influence the resilience of individual trees to drought events. Indeed,
415 differences of drought tolerance seem crucial to understand our results on resistance and recovery. Future
416 studies will need to explore whether the type of hydraulic strategies of the species (Martinez-Vilalta,
417 Lloret, & Breshears, 2012; Tardieu & Simonneau, 1998) ranging from species with more isohydric
418 strategy (e.g. spruce and fir) - reacting rapidly to drought stress by closing stomata (Brodribb & Holbrook,

419 2004; Cruiziat, Cochard, & Améglio, 2002) – to species with more anisohydric strategy (e.g. oak and
420 beech) - reacting much slower to drought, thus risking irreversible organ damage - could explain how
421 species mixing affect drought resilience to environmental conditions (Hochberg, Rockwell, Holbrook, &
422 Cochard, 2018; Pretzsch et al., 2013).

423 **Limits and perspectives**

424 This study focused on two-species mixtures, which allowed us to interpret the results in the light
425 of the interactions between species pairs, but which also necessarily limits the generalization of our
426 findings. Considering other mixed stands and/or wider range of species richness in mixed stands could
427 complement our results. All plots used in this study were composed of mature and closed forests with
428 large basal area to control for the effect of stand structure and total amount of competition. This might
429 explain why *BA* did not affect significantly mean radial growth.

430 We only analyzed tree radial growth whereas forest dynamics will also be affected by volume and
431 height growth, tree mortality and recruitment. We were unable to include tree mortality in our analysis (as
432 our dataset did not allow for this) and this might lead to an underestimation of the drought effect. As the
433 risk of mortality in forest ecosystems could strongly increase in the next decades (Greenwood et al.,
434 2017), it appears especially important to explore this aspect in future studies. More generally, we
435 recommend extending this kind of analyses to other processes of forest dynamics.

436 **Temporal stability and resilience: two complementary approaches**

437 While the proportion of heterospecific trees in its neighbourhood did not affect the mid-term
438 temporal stability of the growth of a tree, it had a significant and “species-dependent” effect on resistance
439 and recovery after drought. Metrics based on the analysis of the mid-term stability of growth can thus
440 hide local mixing effects on the short-term response of trees to extreme events. Our study highlights the
441 merit of analysing short- and mid-term responses of tree growth to evaluate biodiversity effects related to
442 climatic stress. Furthermore, our method allowed us to understand how lagged climatic effects are

443 affected by species interactions, which will be important to better predict the effect of climatic changes on
444 forest ecosystems (Ogle et al., 2015).

445

446 **AUTHORS' CONTRIBUTIONS**

447 XM conceived the original question and field setup of this study. MJ, GK and XM designed the
448 research, developed the methodology; MJ processed and analysed the data; MJ, GK and XM led the
449 writing of the manuscript. All authors contributed critically to the drafts and gave final approval for
450 publication.

451 **DATA ACCESSIBILITY**

452 Data will be deposited in the Dryad Digital Repository

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676

677 **TABLES**678 **Table 1:**

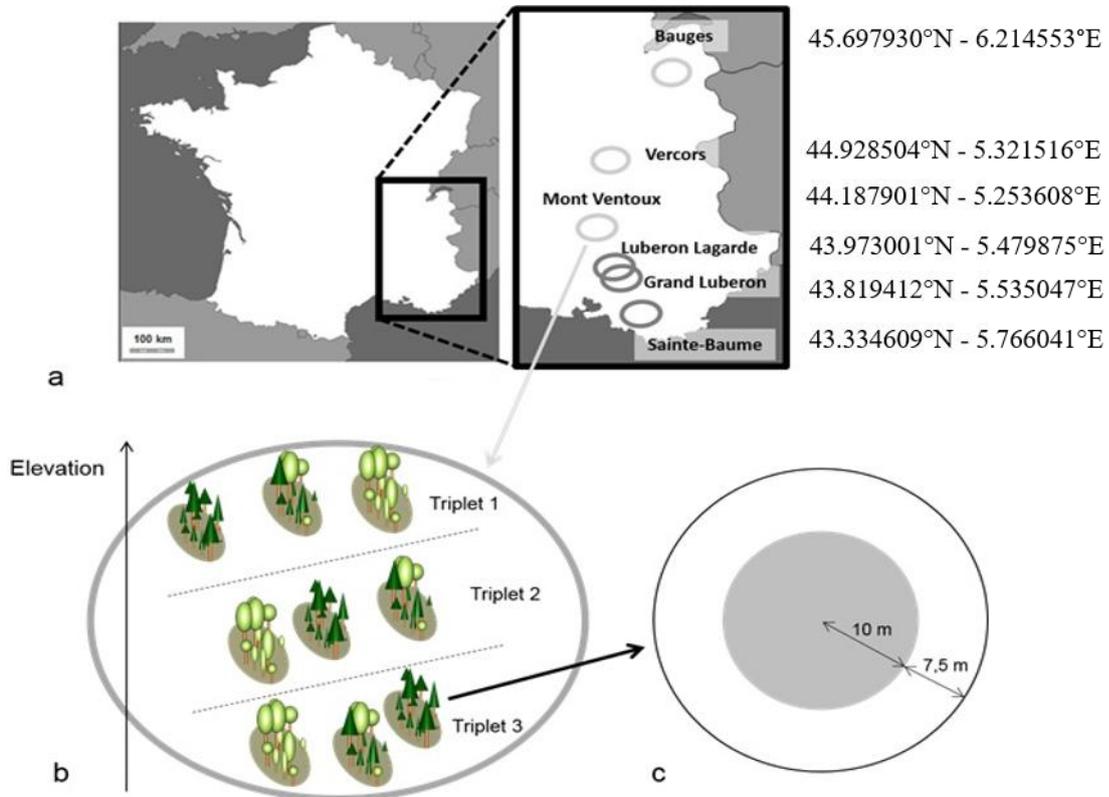
Model	$DBH (c_1)$	$BA (c_2)$	$g_{hete} (c_3)$	<i>Resistance</i> (a)	<i>Recovery</i> (b)	<i>Resistance: g_{hete}</i> (a_{gh})	<i>Recovery: g_{hete}</i> (b_{gh})
Beech (North)	0.049(±0.003) *	-0.00001(±0.00002)	0.126(±0.100)	-0.206(±0.046) *	0.068(±0.018) *	0.025(±0.106)	0.001(±0.043)
Fir	0.040(±0.002) *	0.000004(±0.00001)	0.309(±0.164)	-0.448(±0.036) *	0.051(±0.014) *	-0.232(±0.089) *	0.092(±0.034) *
Beech (South)	-0.033(±0.007) *	0.0001(±0.0001)	-0.806(±0.385) *	-0.427(±0.062) *	0.133(±0.026) *	-0.203(±0.145)	-0.001(±0.061)
Oak	-0.071(±0.007) *	0.00001(±0.00003)	-0.018(±0.085)	-0.276(±0.039) *	0.073(±0.016) *	0.205(±0.100) *	-0.026(±0.043)

679

680 Estimates (± standard deviation) of the linear models tested to explain individual annual BAI for every species with the North and the South parts
681 of the gradient taken separately. North includes plots in Mont Ventoux, Vercors and Bauges, and South includes plots in Luberon Lagarde, Grand
682 Luberon and Sainte-Baume. *DBH* is the diameter at breast height, *BA* is the total basal area of competitors in the neighbourhood of tree, *g_{hete}* is the
683 proportion of heterospecific trees (in percentage of basal area). *Resistance* and *Recovery* are respectively the response to extreme drought and the
684 recovery (from 1 to 4 years) after the extreme drought. *Resistance: g_{hete}* and *Recovery: g_{hete}* are respectively the interaction between the proportion
685 of heterospecific trees and response to extreme drought and the recovery (from 1 to 4 years) after the extreme drought (see Material and Methods
686 section). Significant *p-value* at the 0.05 threshold of *t*-tests are represented by “*”.

687 **FIGURES**

688 **Figure 1**

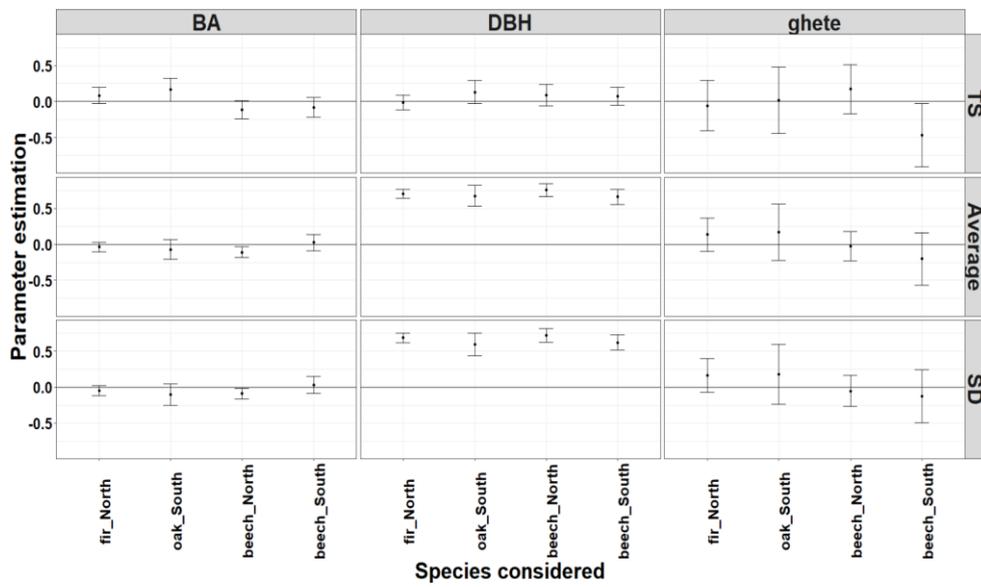


689

690 Locations of the plots with schematic description of the study design. (a) Study area and site locations
 691 where the plots have been sampled. North sites (light grey circles) are Mont Ventoux, Vercors and
 692 Bauges, with plots sampled in beech-fir forests. South sites (dark grey circles) are in Luberon Lagarde,
 693 Grand Luberon and Sainte-Baume, with plots sampled in beech-oak forests. (b) Simplified
 694 representation of a site with three triplets of plots (one plot with monospecific stand of species A
 695 (beech), one plot with monospecific stand of species B (fir or oak), and one plot with mixed stand of
 696 species A and B) distributed along an elevation gradient. (c) Representation of a plot, with a central
 697 area (grey area) in which all trees with a DBH > 7.5 cm were sampled, and an external 7.5m-crown
 698 (buffer zone) in which only the trees with a larger DBH than the median DBH of trees in the central
 699 area have been sampled (dominant trees).

700

701 **Figure 2**



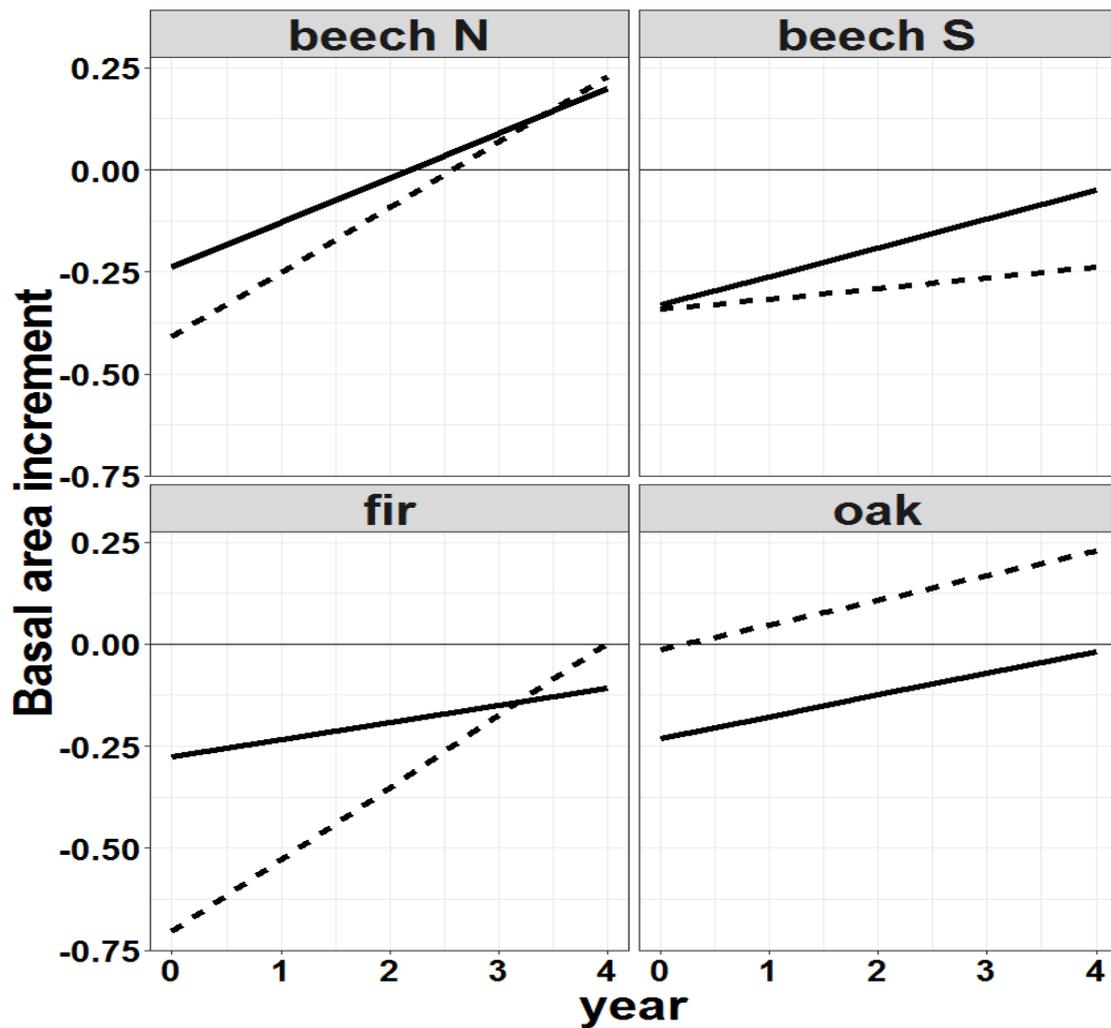
702

703 Estimates of the effect of the explicative variable (BA, DBH and g_{hete}) on temporal stability (TS),

704 average and standard deviation (SD) of basal area increment for each individual model, *i.e.* one model

705 for each species in each part of the gradient: fir (North), beech (North), oak (South) and beech (South).

706



708

709 Response of tree basal area increment after an extreme drought event (year with SPEI < -1.17). Each
 710 plot represents a species and a gradient, with *fir* (fir in North), *beech N* (beech in North), *oak* (oak in
 711 South) and *beech S* (beech in South). Solid and dashed lines are respectively for an individual tree
 712 surrounded by only conspecific ($g_{\text{hete}} = 0\%$) or only heterospecific ($g_{\text{hete}} = 100\%$) trees, corresponding
 713 to both extremes of the percentage of heterospecific in the local neighbourhood.

714