

1 Oak regeneration facing deer browsing : can
2 competition between saplings offset the
3 diversion effect ? A simulation experiment.

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22 1 Abstract

23 The constraint caused by wild ungulates on forest regeneration is increas-
24 ing worldwide. Hypotheses for plant association effects predict that species
25 susceptible to herbivory can gain protection from other neighbouring plant
26 species. In theory, such interactions could help limit the impact of brows-
27 ing on the regeneration of specific tree species. However, the presence of
28 neighbouring species can also result in increasing competition for resources
29 between species. The resultant effects on forest regeneration of these inter-
30 actions, both positive (protection against herbivores) and negative (inter-
31 specific competition) are still unclear.

32
33 To gain insight, we coupled models of browsing by roe deer (*Capreolus*
34 *capreolus*) and of forest dynamics to simulate trajectories of oak (*Quercus*
35 *petraea* (Matt.) Liebl.) regeneration admixed with species of contrasted
36 palatability and growth rate under different scenarios of browsing pressure
37 and initial sapling density. We also investigated how releasing oak saplings
38 from all or specific neighbours during the simulation affect regeneration.

39
40 We found that admixed species composition had a relatively weak effect
41 on the density of oak recruits, but a strong effect on the duration of the
42 regeneration phase. Oak regenerated faster when admixed with species of
43 intermediate growth and low palatability (*Fagus sylvatica*) than with species
44 of fast growth and high palatability (*Carpinus betulus* L.), except at in-
45 termediate sapling density and high browsing pressure where we found the
46 opposite. Releasing oak from all competitors was most effective in promot-
47 ing oak regeneration when admixed with both species together, although the
48 benefit of competition release was much weaker at high browsing pressure.
49 Lastly, we found that at low initial sapling density (*i.e.*, 10 saplings/m²), oak
50 regeneration was driven only by browsing and the effect of admixing species
51 became negligible.

52
53 Our study showed that admixing oak with palatable neighbors impedes
54 rather than improves oak regeneration due to increased competition for re-
55 sources. As such, we suggest that the benefits of herbivore diversion can be
56 off-set by increased inter-specific competition.

57
58 **Key-words:** ungulates, sessile oak, association effects, attractant-decoy

59 hypothesis, forest regeneration, forest dynamics model

60

61 2 Introduction

62 Increasing wild ungulate populations in most of the northern hemisphere has
63 made deer herbivory a major concern for forest regeneration (Linnell & Za-
64 chos, 2011; Beguin *et al.*, 2016; Martin *et al.*, 2020). Management practices
65 such as fencing or culling deer populations can mitigate this effect, but they
66 incur costs. These costs are economic (*e.g.*, high cost of fencing, Löf *et al.*,
67 2021), ecological (*e.g.*, landscape fragmentation or shrub proliferation inside
68 fences, Ward *et al.*, 2018; Baltzinger *et al.*, 2018) and social (*e.g.*, contesta-
69 tion of wildlife management practices by public opinion, Dandy *et al.*, 2012).
70 Identifying alternative practices to ensure the regeneration of tree species
71 most affected by herbivory is thus a crucial challenge for forest managers.
72 Theories of plant association effect assume that plant species may gain pro-
73 tection from the presence of neighboring species that divert herbivory (Pfister
74 & Hay, 1988; Underwood *et al.*, 2014). Accounting for these interactions in
75 forest management practices is increasingly viewed as a promising solution
76 to limit browsing damages. Typical applications would include leaving palat-
77 able sapling competitors (De Vriendt *et al.*, 2020) or even promoting them
78 (Felton *et al.*, 2022) during the cleaning and thinning of production stands to
79 divert browsing pressure towards them. However, maintaining the presence
80 of neighbours may also affect competition patterns between saplings, and the
81 resultant effect on forest regeneration, summing positive interactions (pro-
82 tection against herbivores) and negative ones (inter-specific competition),
83 remains largely unknown.

84

85 Concepts of plant association effects have led to several complementary
86 hypotheses to explain how browsing pressure on an individual plant is related
87 to the relative palatability of its neighbours at different spatial scales. At
88 broad scales (*i.e.*, between feeding patches), the repellent-plant hypothesis
89 (RPH, or associational defence) predicts that plants will gain protection when
90 surrounded by unpalatable neighbours, as these will decrease the chances of
91 the plant feeding patch being visited by herbivores (Hjältén *et al.*, 1993; Bee
92 *et al.*, 2009; Ruttan & Lortie, 2013; Champagne *et al.*, 2018). Conversely,
93 herbivory should increase when the neighbours are more palatable as they

94 attract herbivores to the feeding patch (*i.e.*, associational susceptibility or
95 spillover effect). By contrast, at smaller scales (*i.e.*, within patches), a plant
96 should benefit from being surrounded by more palatable neighbours that will
97 divert browsing pressure towards them (attractant-decoy hypothesis (ADH)
98 or neighbour contrast defence, [Ward *et al.*, 2008](#); [Ruttan & Lortie, 2013](#)),
99 and should experience more damage when surrounded by unpalatable neigh-
100 bours (neighbour contrast susceptibility). A meta analysis showed that these
101 association effects were stronger at small spatial scales, and were dominated
102 overall by association defence (ADH), suggesting that herbivore selection is
103 stronger within than between patches ([Champagne *et al.*, 2016](#)). However,
104 whether forest management practices relying on the ADH - *e.g.*, promoting
105 palatable neighbours in the stand to divert the browsing pressure toward
106 them ([De Vriendt *et al.*, 2020](#); [Felton *et al.*, 2022](#)) - can efficiently improve
107 forest regeneration remains to be determined.

108

109 In practice few studies have tested the effect of leaving palatable tree
110 species as an alternative food resource to promote the regeneration of a
111 crop tree species and they yielded conflicting results ([Stokely & Betts, 2020](#);
112 [De Vriendt *et al.*, 2020](#)). [De Vriendt *et al.* \(2020\)](#) reported that in the pres-
113 ence of moose browsing, spruce regenerated better without mechanical release
114 from competitors, whereas [Stokely & Betts \(2020\)](#) found that controlling
115 the competing vegetation promoted hemlock (*Tsuga heterophylla*) regenera-
116 tion even under deer browsing pressure. [Perea & Gil \(2014\)](#) showed that in
117 sites with high browsing pressure, oak (*Quercus pyrenaica*) regenerated faster
118 when planted under non-preferred rather than palatable shrubs. These re-
119 sults emphasize that leaving neighbouring vegetation as alternative forage
120 results in a balance between facilitation and competition. These effects thus
121 need to be studied jointly to fully understand how surrounding vegetation
122 affects tree regeneration.

123

124 The balance between the facilitative (herbivory diversion) and competi-
125 tive effects exerted by surrounding neighbours on a focal tree species should
126 primarily be driven by the browsing pressure exerted, with a transition from
127 high competition to high facilitation along a gradient from low to high brows-
128 ing pressure. Indeed, the stress-gradient hypothesis (SGH) predicted that
129 consumer-driven associational benefits should be maximal at high consumer
130 pressure ([Bertness & Callaway, 1994](#); [Lortie & Callaway, 2006](#); [Maestre *et al.*,
131 2009](#)). This hypothesis in the context of tree-deer interactions was confirmed

132 by several studies showing higher herbivory diversion by neighboring saplings
133 (Borowski *et al.*, 2021) and shrubs (Perea & Gil, 2014) under high browsing
134 pressure. The balance between competition and facilitation is also likely to
135 depend strongly on neighbour traits. Under the assumptions of the ADH,
136 the presence of neighbours with traits attracting herbivores such as low de-
137 fence and high nutrient content (Felton *et al.*, 2018) should tip the balance
138 towards facilitation. However, the plant vigour hypothesis (Price *et al.*, 2001)
139 and the well-documented trade-off between fast growth and defence against
140 herbivores (Herms & Mattson, 1992; Züst & Agrawal, 2017) suggest that
141 palatable species also tend to grow faster. Under this hypothesis, palatable
142 neighbours could exert a stronger competitive constraint than unpalatable
143 ones by shading saplings of the focal species, which could off-set the benefits
144 of herbivore diversion. In practice however, this trade-off is not always ob-
145 served - *e.g.*, beech and spruce saplings growing faster than fir despite being
146 less palatable (Bernard *et al.*, 2017; Unkule *et al.*, 2022). The neighbour-
147 ing species that best promote regeneration could thus be those that diverge
148 from this general trade-off rule by being palatable yet relatively slow-growing.

149
150 Sessile oak (*Quercus petraea* (Matt.) Liebl., hereafter "oak") is an em-
151 blematic species of European temperate forests. It is valued both for its
152 timber and for the high level of biodiversity supported by oak-dominated
153 forests (Mölder *et al.*, 2019). Deer browsing and interspecific competition for
154 resources are two of the main constraints on oak regeneration (Annighöfer
155 *et al.*, 2015; Petersson *et al.*, 2020; Barrere, 2021). In central Europe, oak
156 frequently co-occurs with beech (*Fagus sylvatica*) and hornbeam (*Carpinus*
157 *betulus* L.), two species known to be more shade-tolerant and faster-growing
158 than oak at the sapling stage (Ligot *et al.*, 2013; Van Couwenberghe *et al.*,
159 2013), so that they must generally be controlled to ensure oak regenera-
160 tion (Von Lüpke, 1998). The two species also differ in both their relative
161 palatability - hornbeam being more frequently browsed than beech or oak
162 (Boulanger *et al.*, 2009; Tixier *et al.*, 1997) - and their growth rate - horn-
163 beam growing more vigorously than beech (Ligot *et al.*, 2013). These three
164 species thus offer an interesting opportunity to gain a better understanding
165 of how tree regeneration is influenced by admixed species composition under
166 different conditions of browsing pressure and sapling density. Here, we tested
167 the following hypotheses:

168

169 H1 *The ideal companion species for oak varies along a gradient of deer*
170 *browsing pressure.* Under a high browsing pressure, the success of oak
171 regeneration (*i.e.*, high density of recruits and short regeneration phase)
172 will be higher when admixed with hornbeam, which is more palatable,
173 as predicted by the ADH. Conversely, oak regeneration success will be
174 higher when admixed with beech under low browsing pressure, since
175 beech is less vigorous than hornbeam.

176 H2 *The optimal management of oak competitors varies along a gradient*
177 *of deer browsing.* Under high browsing pressure, the success of oak
178 regeneration will be higher when the most palatable competitors are
179 left in place during the regeneration phase, since they will divert the
180 browsing pressure towards them. Conversely, under low browsing pres-
181 sure, releasing oak from all competitors will improve the quality of its
182 regeneration.

183

184 Testing these hypotheses required crossing different levels of seedling den-
185 sity, browsing pressure and regeneration species composition, which is par-
186 ticularly difficult to control in field conditions. We therefore opted for a
187 simulation approach coupling models of deer browsing and a model of forest
188 dynamics. We calibrated the models with field and literature data to take
189 into account species-specific palatability and growth.

190 3 Materials and methods

191 3.1 The RRESHAR model

192 *Model presentation* - RReShar (Regeneration and Resource Sharing) is a
193 model simulating forest dynamics implemented on the Capsis modelling plat-
194 form (Dufour-Kowalski *et al.*, 2012) and described in chapter 7.3.2 of Barrere
195 (2021) and chapter 4 of Gaudio (2010). It simulates the regeneration and
196 dynamics of forest stands based on resource exchanges (*i.e.*, light and water)
197 among different vegetation compartments (saplings, understory vegetation
198 and adult trees). In this study, we focused on light sharing between saplings
199 (*i.e.*, individual trees less than 6 m in height) and adult trees (but see Helluy,
200 2020, for a description of water exchanges). The model is spatially explicit:
201 adult trees and saplings are positioned in a grid of cells (9 x 9 square cells of
202 area 9 m² in the present study) and have exact individual coordinates (see
203 supporting information A for a graphical representation of a RReShar scene).
204 Both are characterized by their height and stem diameter. Survival, height
205 and diameter growth of adult trees and saplings are modelled with a yearly
206 time step according to species identity, initial size, and light availability.

207
208 *Light exchanges* - The interception of light by adult trees is modelled
209 by the SamsaraLight library of Capsis, which algorithm was first described
210 by Courbaud *et al.* (2003) and more recently by Ligot *et al.* (2014). The
211 model simulates the transmission of direct and diffuse light rays through tree
212 crowns. Transmittance (percentage of above canopy light transmitted to the
213 understory, *PACL*) is computed with a daily time step throughout the plots
214 and targets every cell centre. For a given light ray, the radiation transmitted
215 to the understory is a function of the shape and porosity of the crown fol-
216 lowing a Beer-Lambert law (Courbaud *et al.*, 2003). Under the tree canopy,
217 a fraction of light is intercepted by each sapling of the cell successively from
218 the tallest sapling following the equation linking tree basal area to light in-
219 terception developed in Sonohat *et al.* (2004):

220

$$PACLb_i = PACLa_i \times e^{-k_i G} \quad (1)$$

221 where $PACLa_i$ and $PACLb_i$ are respectively the transmittance above and
222 below sapling i , k is the species coefficient of extinction, and G is the basal
223 area per unit area of the sapling. Within a cell, the spatial variability of

224 light availability was neglected: the amount of light received by a sapling
 225 thus only depended on its height and not on its position.

226

227 *Browsing* - In this study, we opted to focus on within-patch selection be-
 228 cause between-patch selection has been shown to have much less impact on
 229 browsing probabilities than within-patch selection (Champagne *et al.*, 2016).
 230 The browsing pressure (quantified as a dry biomass of saplings browsed per
 231 hectare and per year, specified by the user) was therefore constant across
 232 all cells of the grid, but with different browsing probabilities for each sapling
 233 within the cell, calculated as a function of sapling height and species identity.
 234 We also focused on browsing by roe deer (*Capreolus capreolus*), the main un-
 235 gulate herbivore in the study sites used to calibrate the browsing probability
 236 equations (Barrere *et al.*, 2021).

237

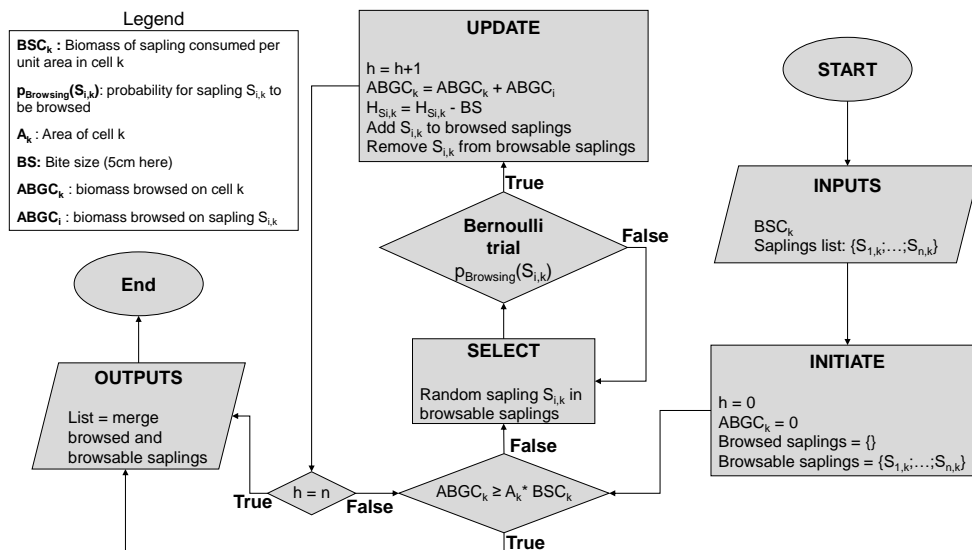


Figure 1: Flowchart of the algorithm implemented in RReShar to model sapling browsing at the cell level. See text for details on each process.

238 In a given cell, saplings with higher browsing probabilities were preferen-
 239 tially browsed (see Fig. 1). Browsed saplings lost 5 cm in their annual height
 240 growth, which is the mean bite size (BS) based on roe deer rumen analysis (S.
 241 Saïd, unpublished data). Each bite corresponds to a specific above-ground
 242 biomass consumed (AGBC) calculated as: $AGBC = \beta_1(D^2)^{\beta_2} \times (BS/H)$

243 (where D is the sapling diameter (mm), H its height (cm), and β_1 ad β_2 are
 244 species-specific biomass coefficients from [Annighöfer et al. \(2016\)](#) reported in
 245 Table 1). Saplings were selected for browsing either until all the saplings in
 246 the cell had been browsed once, or when the accumulated browsed biomass
 247 reached the threshold of browsed biomass per hectare and per year specified
 248 for the simulation (Fig. 1).

249

250 *Understory management* - In the model, a clearing operation targeting a
 251 competitive species s consisted in cutting at 20 cm 80% of sapling species s
 252 in the scene. We repeated these clearing operations every 4 years, starting
 253 in Year 5 of the simulation.

254

255 3.2 Model calibration

256 *Sapling growth*: we calculated annual height increment (iH , in cm) for oak
 257 (*Quercus petraea* (Matt.) Liebl.), beech (*Fagus sylvatica*) and hornbeam
 258 (*Carpinus betulus* L.) saplings as a function of the percentage of above canopy
 259 light ($PACL$) and of sapling initial height (H_0 , in cm) following the equation
 260 from [Ligot et al. \(2013\)](#):

$$iH = \frac{a_1 \times \sqrt{H_0}}{1 + e^{1 - \frac{PACL}{a_2}}} \quad (2)$$

261 where a_1 and a_2 are species-specific coefficients obtained from [Ligot et al.](#)
 262 (2013), given in table 1. We reanalyzed the data of [Ligot et al. \(2013\)](#) to fit
 263 the same equation for hornbeam saplings which were not originally studied
 264 (supporting information B). Fig. 2.b. shows the annual growth in height for
 265 the three studied species. Diameter increment (iD , in mm) was calculated
 266 based on allometric relations between height and diameter (*i.e.*, $iD = b_1 \times iH$,
 267 where b_1 is a species-specific parameter reported in table 1). We calculated
 268 coefficient b_1 for each species with a reanalysis of the data from [Ligot et al.](#)
 269 (2013), presented in supporting information C.

270

271 *Survival* - Estimating survival requires continuous monitoring over time
 272 of individuals, which is common for adult trees but rarely done on saplings
 273 owing to their high numbers. In the absence of such data, we modelled
 274 survival probability (p_s) as a function of sapling initial height (H_0) as:

$$\log\left(\frac{p_s}{1-p_s}\right) = c_1 \times H_0 + c_2 \quad (3)$$

275 where c_1 and c_2 are parameters set arbitrarily so that the densities of
 276 saplings observed at the end of the simulations are consistent with those ob-
 277 served in the data used to calibrate the model (supporting information D).
 278 We used the same parameter values for all three species (table 1).

279
 280 *Browsing probabilities* - Annual browsing probabilities for roe deer were
 281 calibrated using field data from [Barrere et al. \(2021\)](#). The experiment in-
 282 cluded exhaustive vegetation surveys in 1 m² plots where the percentage of
 283 cover and browsing occurrence were noted for each species at three different
 284 height classes (0-50cm, 50-130cm and 130-300cm). From these data, brows-
 285 ing probability for each species was modelled with the following equation:

$$p = \begin{cases} 0 & \text{if } H_0 \in [0\text{cm} - 20\text{cm}[\\ d_1 + d_2 \times H_0 & \text{if } H_0 \in [20\text{cm} - 130\text{cm}] \\ 0 & \text{if } H_0 > 130\text{cm} \end{cases} \quad (4)$$

286 where H_0 is sapling initial height, and d_1 and d_2 are species-specific coef-
 287 ficients obtained from [Barrere \(2021\)](#) and reported in table 1. The analytical
 288 approach and detailed methodology to calculate these coefficients for each
 289 species are presented in details in [Barrere \(2021\)](#). We set the browsing prob-
 290 ability at 0 for saplings of less than 20 cm in height or higher than 130 cm
 291 (Fig. 2.a). This choice is supported by empirical data, particularly the study
 292 by [Nichols et al. \(2015\)](#), which showed that under similar ecological condi-
 293 tions (*i.e.*, lowland temperate deciduous forests), browsing by roe deer was
 294 very rarely observed beyond this sapling height range.

295

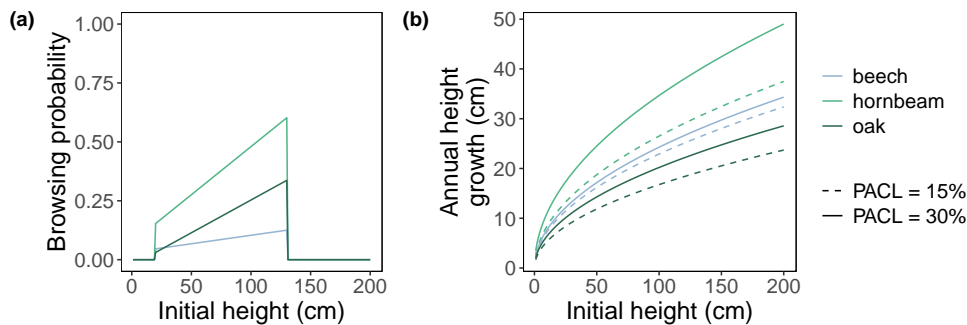


Figure 2: Model predictions of (a) annual browsing probabilities by roe deer and (b) sapling annual height growth (cm/year).

Table 1: Parameters of the models for growth, survival, and browsing probability, respectively corresponding to Eq. 2, 3, and 4, and source to obtain each parameter.

	Oak	Beech	Hornbeam	Source
β_1	0.67311	0.62342	0.35633	Annighöfer et al. (2016)
β_2	0.85202	0.87409	0.92508	Annighöfer et al. (2016)
a_1	2.059	2.431	3.646	Ligot et al. (2013) and appendix A
a_2	6.058	3.964	7.577	Ligot et al. (2013) and appendix A
b_1	0.079	0.093	0.093	re-analysis of Ligot et al. (2013) (appendix B)
c_1	0.05	0.05	0.05	set to obtain realistic density (appendix C)
c_2	-0.6	-0.6	-0.6	set to obtain realistic density (appendix C)
d_1	-0.025	0.0007	0.004	Section 7.3.4.3 of Barrere (2021)
d_2	0.0028	0.0332	0.072	Section 7.3.4.3 of Barrere (2021)

296 3.3 Simulation experiment

297 *Silvicultural scenarios* - The simulated silviculture mimicked the French guide-
 298 lines to regenerate oak in evenaged stands ([ONF, 2010](#)). Once the stand is
 299 mature and after a mast year, a seeding cut is made to remove 25-50% of the
 300 stand basal area, open the canopy and provide sufficient light for seedlings
 301 to grow while maintaining seed trees in the stand to ensure a minimal flow
 302 of seeds. The remaining adult trees are harvested once the regeneration is
 303 well established (*i.e.*, the cohort of saplings have grown to above 1.30 m in

304 height). The simulations start in Year 1 after the seeding cut (*i.e.*, with one-
305 year-old seedlings established) until Year 20, just before the final harvest of
306 the adult stand.

307

308 *Initial scene* - Because the simulations focused on the short-term regen-
309 eration dynamics, we did not need to include a structurally complex canopy
310 cover. We therefore initialised the stand with homogeneously distributed
311 adult oak trees of equal diameter and height, resulting in a stand basal area
312 of $5 \text{ m}^2 \cdot \text{ha}^{-1}$ and a *PACL* below the canopy of 35% at the initialization.
313 The modelled scene consisted of a square plot of area 729 m^2 divided into
314 81 square cells each of area 9 m^2 . For all species, the height and diameter
315 of saplings at the initialization was set randomly, based on the joint height
316 diameter distribution of one-year-old saplings in the three French study sites
317 in [Barrere et al. \(2021\)](#).

318

319 *Range of sapling density and browsing pressure* - The initial density of
320 saplings ranged from 10 to 50 saplings/ m^2 . These initial densities reflected
321 the range observed in the data used to calibrate the growth model (sup-
322 porting information D) and were consistent with the range of initial sapling
323 densities observed in field studies conducted in similar conditions (*e.g.*, see
324 [Van Couwenberghe et al., 2013](#); [Collet et al., 2017](#)). For browsing, we chose
325 three levels of biomass yearly browsed: 0, 75 and $150 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$. Our ap-
326 proach to model the biomass browsed on a sapling assumes that above-ground
327 biomass is homogeneously allocated vertically, from the collar to the apical
328 bud, which likely overestimates the biomass browsed. Instead of choosing
329 browsing pressure values that are consistent with the true nutritional needs
330 of roe deer (*i.e.*, approximately 0.5kg per day based on [Drożdż & Osiecki](#)
331 [\(1973\)](#)), we have set values of browsing pressure so that the browsing rates
332 observed in the simulations matches those observed in field conditions. For
333 an average stand (*i.e.*, 100% oak, an initial density of 30 sapling/ m^2 and a
334 quadratic diameter of saplings of 20 mm), 75 and $150 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ cor-
335 respond respectively to 25% and 75% of saplings browsed (see supporting
336 information E), consistently with the range of browsing rates observed in
337 other studies ([Morellet et al., 2001](#); [Boulanger et al., 2009](#); [Petersson et al.,](#)
338 [2020](#)).

339

340 *Simulations* - To investigate how admixed species affected oak regenera-
341 tion at different browsing pressure (H1), we ran simulations without clearing

342 and with varying initial species compositions (oak admixed with beech, horn-
343 beam, or both species), densities and browsed biomass per year (see Table
344 2). To investigate how the clearing of admixed species affected oak regen-
345 eration under different browsing pressure (H2), we ran simulations with a
346 fixed initial seedling composition (33% of oak, beech and hornbeam) and
347 varying browsed biomass, initial seedling densities and clearing levels (see
348 table 2). We replicated each treatment combination (36 for H1 and 27 for
349 H2) 10 times, to take into account the different sources of stochasticity in
350 the models, *i.e.*, initial size distribution of saplings based on the joint height
351 diameter distribution in the data, and during the selection of saplings for
352 browsing and for clearing operations. This resulted in a total of 630 simula-
353 tions (360 for H1, 270 for H2).

354

Table 2: Levels of the simulation factors tested for each hypothesis. Each factor combination was replicated 10 times.

	Initial species composition	Biomass browsed annually	Initial sapling density	Species cleared
H1	(1) 50% QP - 50 % FS	(1) 0 kg.ha ⁻¹	(1) 10 m ⁻²	(1) none
	(2) 50% QP - 50 % CB	(2) 75 kg.ha ⁻¹	(2) 30 m ⁻²	
	(3) 50% QP - 25 % FS - 25% CB	(3) 150 kg.ha ⁻¹	(3) 50 m ⁻²	
	(4) 100% QP			
H2		(1) 0 kg.ha ⁻¹	(1) 10 m ⁻²	(1) FS
	(1) 33% QP - 33 % CB 33% FS	(2) 75 kg.ha ⁻¹	(2) 30 m ⁻²	(2) CB
		(3) 150 kg.ha ⁻¹	(3) 50 m ⁻²	(3) none

QP: *Quercus petraea*; FS: *Fagus sylvatica*; CP *Carpinus betulus*;

355 3.4 Data analysis

356 *Metrics of oak regeneration success* - As we modelled only the trajectory of
357 a single cohort of saplings, the time course of the density of oak saplings
358 above 130 cm (when saplings become too high to browse based on [Nichols](#)
359 [et al. \(2015\)](#)) generally resembled a logistic curve: after a few years at zero
360 it increased rapidly before levelling off (Fig. 3). To quantify the success
361 of oak regeneration, we used one metric related to the maximum density of

362 oak saplings recruited (DR_{max}) and one metric related to the regeneration
363 duration (time T_{half} to reach half DR_{max}) (Fig. 3).

364

365 *Analyses for H1* - For each of the three initial densities tested, we fitted
366 two analyses of variance (ANOVA): one with DR_{max} and one with T_{half} as
367 response variable. For each response variable and each density (six models
368 in all), we included three factors: browsing treatment, species composition,
369 and the interaction between them. In addition of these six models that ex-
370 amine the relative impact of species composition and browsing on DR_{max}
371 and T_{half} , we also fitted for each level of sampling density and browsing sim-
372 ilar ANOVAs with only species composition as explanatory variable, to test
373 the significance of the species composition effect for a given level of browsing.

374

375 *Analyses for H2* - For each of the three initial densities tested, we fitted
376 two ANOVAs: one with DR_{max} and one with T_{half} as response variable. For
377 each response variable and each density (six models in all), we included three
378 factors: browsing treatment, clearing treatment, and the interaction between
379 them. As for H1, we also ran ANOVAs to test the significance of the clearing
380 treatment at each level of browsing.

381

382 As both response variables in all statistical models were continuous but
383 strictly positive, we used a log transformation to match the assumption of a
384 Gaussian error distribution. In the models with R_{max} as response variable,
385 we also added a constant lower than the minimum non-zero value ($c = 0.001$)
386 before log-transformation, which assumes a very small recruitment even in
387 plots where no sapling was recruited. The log plus constant transformation
388 is common in analyses of variance to deal with zero values (Berry, 1987).
389 Since the value chosen for the constant may in some cases affect the model
390 coefficients, we verified that the statistical results were stable by fitting the
391 same models for different values of this constant (*i.e.*, 0.01, 0.0001), which
392 yielded very similar results with only negligible changes in F-values (analysis
393 not shown). We graphically checked that residuals were normally distributed
394 for each model using quantile-quantile plots (see supporting information F).
395 All statistical analyses were performed with R statistical software, version
396 4.1.2 (RCoreTeam, 2019).

397

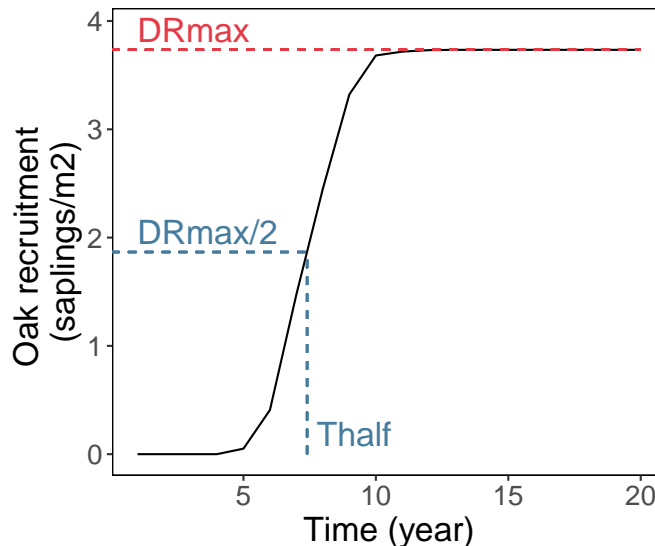


Figure 3: Changes over time in the density of oak saplings above 130 cm during a simulation. DR_{max} and T_{half} are respectively the maximum density reached and the time to reach half the maximum density.

398 4 Results

399 4.1 Species composition effect on oak regeneration

400 *Effect on maximum density of oak recruits (DR_{max})* - At low sapling density
 401 (10 saplings/m²), admixed species composition had a significant effect of low
 402 magnitude on the density of oak recruits ($F = 7.2$, $p < 0.01$) which was driven
 403 mostly by the browsing pressure ($F = 9672.8$, $p < 0.01$). At both interme-
 404 diate (75 kg.ha⁻¹.year⁻¹) and high (150 kg.ha⁻¹.year⁻¹) browsing pressure,
 405 no oaks were recruited after 20 years of simulation, except a few individuals
 406 when accompanied with hornbeam at intermediate browsing pressure (Fig.
 407 4.a).

408 At intermediate sapling density (30 saplings/m²), maximum density of oak
 409 recruits was also primarily driven by browsing ($F = 1719.5$, $p < 0.01$). Initial
 410 species composition had a small effect ($F = 525.3$, $p < 0.01$) that interacted
 411 significantly with browsing ($F = 388.8$, $p < 0.01$), with more abundant oak
 412 recruits when oak was accompanied by hornbeam than with beech but only
 413 at high browsing pressure (Fig. 4.b).

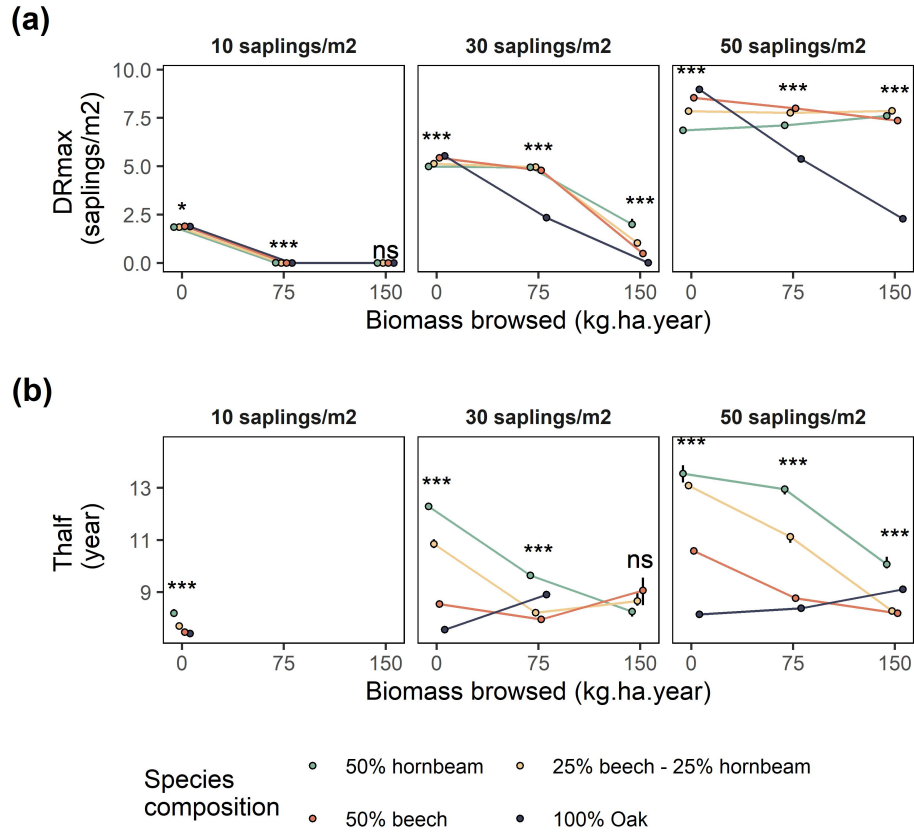


Figure 4: Effect of browsing pressure and initial species composition on the maximum oak sapling density recruited (DR_{max}) and the time to reach half that density (T_{half}) for different initial sapling densities. Points show DR_{max} and T_{half} averaged across the 10 replicates of each scenario. Error bars, that show 0.025 to 0.975 quantiles in the data, are not always visible due to the low within-scenario stochasticity relatively to variations in DR_{max} and T_{half} between scenarios. * and *** respectively indicate a significant effect of species composition for a given seedling density and browsing pressure at $\alpha = 0.05$ and $\alpha = 0.001$.

414 In dense clump (50 saplings/m²), species composition had a stronger effect
 415 on the density of oak recruits at low browsing pressure (Fig. 4.a). In these
 416 conditions, it recruited better when admixed with beech than with hornbeam.

417

418 *Effect on recruitment duration (T_{half})* - T_{half} could not be calculated
419 when the density of recruits was zero. Since at low initial density, all simula-
420 tions resulted in a density of oak recruits equal to zero (except in the absence
421 of browsing), we could not fit a T_{half} model. Species composition had a strong
422 consistent effect on regeneration duration at both intermediate ($F = 8.5$, p
423 < 0.01) and high ($F = 9615$, $p < 0.01$) sapling density. Oak regeneration
424 was almost systematically longer when oak was accompanied by hornbeam,
425 and shorter with beech and this effect was stronger at low browsing pressure
426 (Fig. 4). The effect of species composition was systematically stronger on
427 T_{half} than on DR_{max} .

428 **4.2 Effect of clearing operations on the density of oak** 429 **recruits**

430 *Effect on maximum density of oak recruits (DR_{max})* - At low initial sapling
431 density, only browsing had a significant effect on DR_{max} ($F = 15356.1$, p
432 < 0.01), which was not affected by clearing operations ($F = 1.7$, $p = 0.2$).
433 At intermediate sapling density, clearing operations had a weak effect on
434 DR_{max} , and only at high browsing pressure: DR_{max} was approximately 0.5
435 saplings/m² lower when clearing was applied on beech or both species than
436 when applied on hornbeam only (Fig. 5). At high sapling density, clearing
437 operations were by far the main factor driving the density of oak recruits (F
438 $= 555.6$, $p < 0.01$), although this effect tended to be lower at high browsing
439 pressure. The density of oak recruits was systematically higher when both
440 beech and hornbeam were cleared, and lower without clearing or when only
441 beech was cleared (Fig. 5.c).

442
443 *Effect on regeneration duration (T_{half})* - Since at low initial density, all
444 simulations resulted in a density of recruits equal to zero (except in the
445 absence of browsing), we could not fit a T_{half} model. Clearing both beech
446 and hornbeam strongly shortened regeneration duration whereas the absence
447 of clearing or clearing on beech only resulted in the longest regeneration
448 duration at both intermediate ($F = 3451$, $p < 0.01$) and high ($F = 7334$,
449 $p < 0.01$) sapling density. This effect of clearing tended to decrease with
450 increasing browsing pressure (Fig. 5). Across the scenarios of initial sapling
451 density, the regeneration time was comparable overall (8-13 years), but the
452 density of recruits was highly variable (0 -1 sapling/ m² at low initial density,

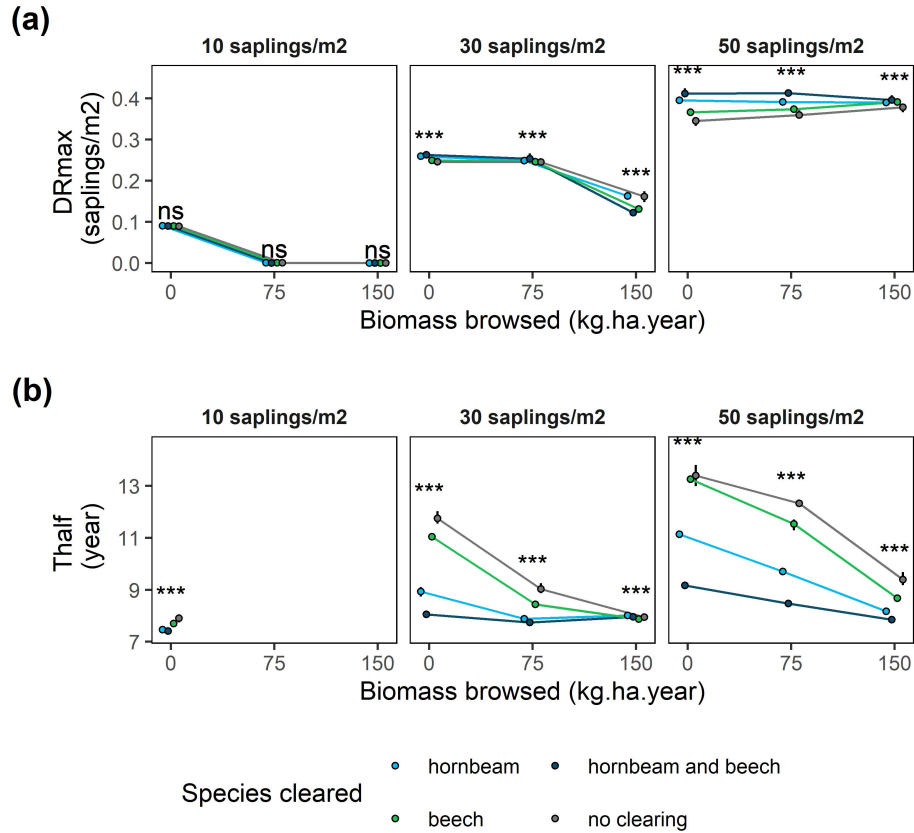


Figure 5: Effect of clearing treatment and browsing on (a) the maximum density of oak recruits (DR_{max}) and (b) the time to reach half that density (T_{half}) for different initial sapling densities. Points show DR_{max} and T_{half} averaged across the 10 replicates of each scenario. Error bars, that show 0.025 to 0.975 quantiles in the data, are not always visible due to the low model stochasticity relatively to variations in DR_{max} and T_{half} between scenarios. * and *** respectively indicate a significant effect of species composition for a given seedling density and browsing pressure at $\alpha = 0.05$ and $\alpha = 0.001$.

453 4.5-5.5 sapling/m² at high densities).

454 5 Discussion

455 A modelling approach enabled us to jointly manipulate three key drivers
456 of oak regeneration, namely browsing pressure, initial sapling density, and
457 species composition (Kohler *et al.*, 2020), and thus to disentangle their re-
458 spective effects and interactions, which is hardly achievable in field condi-
459 tions. This is particularly true for the effect of browsing: deer abundance
460 is hard to estimate reliably (Pfeffer *et al.*, 2018; Forsyth *et al.*, 2022), and
461 so natural gradients of browsing pressure are rarely exploited. The experi-
462 mental manipulation of deer density is technically feasible (*e.g.*, see Horsley
463 *et al.*, 2003) but has a prohibitive financial cost. Simulation experiments
464 thus offer a particularly useful approach to study the effect of browsing on a
465 more continuous scale than with fenced-*un*fenced plots, which remains scant
466 in the literature (Jorritsma *et al.*, 1999; Kramer *et al.*, 2003; De Jager *et al.*,
467 2017).

468

469 5.1 Facilitation is generally off-set by competition

470 Under the conditions of our model, the density of oak recruits depended
471 mostly on browsing pressure and initial seedling density and, to a lesser ex-
472 tent, on regeneration composition. This is in line with field studies showing
473 that browsing intensity (Horsley *et al.*, 2003; Tremblay *et al.*, 2007) and the
474 initial density of seedlings (Kohler *et al.*, 2020) are first-order drivers of the
475 density of recruits. Consistent with our hypothesis H1, the "ideal" compan-
476 ion species for oak varied with the browsing pressure exerted, but not in
477 the magnitude expected. Indeed, our model was built under the assump-
478 tions of the attractant-decoy hypothesis (Ward *et al.*, 2008; Ruttan & Lortie,
479 2013), limiting herbivore selection to within-patches. We therefore expected
480 that under higher browsing pressure, admixing oak with a more palatable
481 species would improve its regeneration by diverting the browsing pressure
482 from oak. At intermediate initial sapling density, we did find a faster and
483 denser oak regeneration when oak was admixed with hornbeam, the most
484 palatable species, consistently with a previous field study conducted in sim-
485 ilar conditions of initial sapling density (Dietz *et al.*, 2022). However, this
486 scenario only occurred at intermediate sapling density and at the highest
487 level of browsing pressure. At high sapling density, oak regeneration was
488 always faster when admixed with beech, a species less palatable but slower-

489 growing than hornbeam (Ligot *et al.*, 2013), even at the highest level of
490 browsing pressure. Although the effect of species composition on oak re-
491 generation overall decreased with increasing browsing pressure, this suggests
492 that under high browsing pressure, the higher palatability of hornbeam is
493 not always sufficient to compensate for its higher competitive effect on oak
494 through light interception. This would be consistent with the idea that fast
495 growing species, even browsed, grows faster than slower growing species that
496 are left unbrowsed (Kupferschmid *et al.*, 2022). From a broader perspective,
497 our results suggest that even under chronic deer browsing, the recruitment of
498 a focal tree species is more strongly driven by the growth rate of its neighbors
499 than by their relative palatability.

500

501 The fact that oak regenerates faster when admixed with beech in most
502 simulations involving browsing may also arise from some of the simplifications
503 of our competition model that mostly rely on the height hierarchy between
504 saplings, without accounting for inter-specific differences in survival, light
505 interception or below ground competition. The fact that our model included
506 a strong difference in browsing probabilities between tall and small saplings
507 while light interception was mostly dependant on seedling size promotes the
508 competitive effect of fast-growing species like hornbeam. Although the rela-
509 tion between browsing probability and seedling height in our model was cal-
510 ibrated with field data, this relation remains highly context-dependent and
511 different relations (e.g., non-linear, lower effect of seedling height) were ob-
512 served in other studies (*e.g.*, see Bergquist *et al.*, 2009; Nichols *et al.*, 2015).
513 Beech could have appeared as a stronger competitor if we had taken into
514 account species-specific differences in survival rates and light interception.
515 Indeed, shade tolerant and fast growing species such as beech and hornbeam
516 are known to intercept light more efficiently (Niinemets, 2010) and to have
517 higher survival rates than less shade-tolerant species like oak (Kobe *et al.*,
518 1995). As the effect of the presence of neighbouring species during regenera-
519 tion is generally only studied in terms of competition (Von Lüpke, 1998) or
520 of herbivore diversion (Champagne *et al.*, 2016; Bee *et al.*, 2009), our sim-
521 ulation approach is a first step in investigating the subtle balance between
522 competition and facilitation, and shows that this balance can be highly sen-
523 sitive to browsing pressure. The results of these simulations must, however,
524 be interpreted with a clear awareness of the different model assumptions.

525

5.2 The benefit of releasing oak from competition decreases with browsing pressure

According to the attractant-decoy hypothesis (Ward *et al.*, 2008; Ruttan & Lortie, 2013), it has been suggested that maintaining and even promoting the presence of palatable neighbours through forest management could reduce browsing damages by diverting herbivory from the focal species (De Vriendt *et al.*, 2020; Felton *et al.*, 2022). Under the conditions of our model, clearing operations to release oak from competition improved its regeneration in nearly all scenarios at variance with our initial hypothesis H2. This result is consistent with previous studies showing that the protective effect of neighbours is not sufficient to balance their competitive effect (Bergquist & Örlander, 1998; Stokely & Betts, 2020). However, it is noteworthy that the benefits of clearing operations strongly decreased with increasing browsing pressure. Given the high economic costs associated with the protection of seedlings from both browsing (*e.g.*, with fences, Löf *et al.*, 2021) and competition (*i.e.*, with clearing), our results suggest that setting up protection against browsing may not necessarily be economically worthwhile at high seedling density. But as our results were obtained with a simulation approach that simplifies the processes of deer browsing and competition, simple field experiments testing this specific question - as in De Vriendt *et al.* (2020) - along with monitoring plots in the context of oak regeneration would be necessary to support this inference. With the addition of economic data, the model we have developed could however be a useful basis to carry out cost-benefit economic analyses, which are critical to fully address the issue of forest management in the context of increasing ungulate populations (Boulanger & Rakotoarison, 2013).

5.3 Higher association effects at high seedling density

Field studies have suggested that the intensity of association effects increases with physical stress such as competition (Underwood *et al.*, 2014). In our simulations, we also observed that oak regeneration was more strongly affected by the composition of the surrounding vegetation at high initial sapling densities, and thus high competition. This result likely reflects that including in our model fixed biomass browsed per unit area and assigning browsing probabilities to saplings, represents relatively well the higher selectivity of ungulates when resource availability is high (Borkowski *et al.*, 2017; Kupfer-

561 [schmid *et al.*, 2022](#)). Indeed, in a context of low sapling density and high
562 browsing pressure, all saplings end up eventually browsed, hindering recruit-
563 ment. Similar situations, referred to as browsing lawns, have been observed
564 in field studies, where saplings are trapped within the reach of ungulates
565 ([Cromsigt & Kuijper, 2011](#)).

566

567 Our food selection model remained nonetheless incomplete as we assumed
568 a constant browsing pressure across cells to focus on within-patch selection.
569 In reality, patch selection can be strongly influenced both by sapling species
570 composition and by the abundance of available forage ([Bee *et al.*, 2009](#); [Kuijper *et al.*, 2009](#); [Champagne *et al.*, 2018](#)). In particular, a higher density of
571 saplings should lead to a higher browsing pressure (though [Borowski *et al.*, 2021](#)
572 did find the opposite pattern), implying that the scenarios we sim-
573 ulated are not all equally likely. Including between-patch selection would
574 require prior knowledge of the relation between forage availability and her-
575 bivory pressure, which has been widely studied in the context of seed preda-
576 tion (*e.g.*, see [Bogdziewicz *et al.*, 2018](#); [Barrere *et al.*, 2020](#)) but rarely for
577 browsing on saplings. Developing field experiments to calibrate this relation
578 would offer key perspectives for the development of our model.

580

581 **6 Conclusion**

582 Taken together, the results from our simulations suggest that it is not always
583 beneficial for oak saplings to be surrounded by palatable neighbours because
584 the diversion of the browsing pressure can be offset by higher inter-specific
585 competition even at high browsing pressure. Under the conditions of our
586 model, we also show that species composition remains a second-order driver
587 of oak regeneration, far behind browsing intensity. Lastly, our model illus-
588 trates once again how simulation experiments can improve our understanding
589 of the relation between ungulates and forest regeneration. This seems par-
590 ticularly crucial in a context of global changes where forests are exposed to
591 an increasing number of biotic and abiotic stresses.

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600 BRE].

601 **8 Conflict of interests**

602 The authors have no conflict of interest to declare.
603

604 **9 Author contribution**

605 JB, GL, BC, AM and PB conceived ideas and designed methodology; JB,
606 GL, BC, FDC and PB developed the model. GL, SS and PB provided data
607 for the calibration of the model. JB ran the simulations, analysed the data
608 and led the writing of the manuscript. All authors contributed critically to
609 the drafts and gave final approval for publication.
610

611 **10 Data availability statement**

612 The code of RReShar, as all models implemented in the Capsis modelling
613 platform, is publicly accessible after having downloaded and installed Cap-
614 sis (<https://capsis.cirad.fr/capsis/download>). The R code to run the
615 simulations and analyses from this paper is available on github at <https://github.com/jbarrere3/CapsisBrowsing>. Note that the hypotheses H1
616 and H2 in the manuscript are respectively referred to as H4 and H3 in the
617 code.
618
619

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