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2 Herbivore-induced branching increases sapling survival in temperate forest canopy gaps

3

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14 The data will be deposited under the following data repository link:

15 <https://github.com/mripasteam/branching>

16

17 Author Contributions statement

18 BJ, MC acquired funding for the experiment; MC, DK, JPMG, BJ designed the experiment,

19 MC, JPMG, TCD, DK conceived the ideas and designed methodology; MC, DPJK collected

20 the data; JWB and MC analysed the data; TCD, JWB, MC created figures; TCD artwork; MC,

21 JPMG and DPJK led the writing of the manuscript. All authors contributed critically to the

22 drafts and gave final approval for publication.

24 1) Tree architectures reflect the main abiotic and biotic selection pressures determining tree
25 growth and survival. Studies have shown that trees growing in herbivore-dominated
26 ecosystems, such as savannas, develop denser, more divaricate ‘cage’-like architectures in
27 response to chronic browsing pressure (also known as ‘brown-world’ architectures). In
28 contrast, trees growing under resource-limited conditions develop traits that allow them to
29 better compete for abiotic resources (referred to as ‘green world’ architectures); for
30 example, light limitation can induce trees to form more pole-like structures that allow them
31 to grow faster in height). In temperate forests, abiotic drivers, and particularly light
32 limitation, have traditionally been assumed to be the main factors affecting plant
33 architecture. However, gap dynamics typically characterize old-growth temperate forest
34 systems, where disturbances such as storms create gaps with temporary high light
35 availability, but also attracting intense mammalian browsing. Under such conditions, one
36 would expect tree saplings to exhibit high architectural plasticity enabling them to develop
37 a ‘cage’ in response to high herbivore pressure, but when herbivore pressure declines
38 switch to a more pole-like structure that allows them to grow quickly in height and compete
39 for light.

40 2) We tested the ability of five dominant European tree species to induce a ‘cage’ architecture
41 (hereafter referred to as ‘cage plasticity’) under contrasting light and herbivory regimes in
42 a full-factorial experiment in Białowieża Forest. We planted 720 young tree saplings in six
43 replicated blocks in which we manipulated ungulate browsing (exclosure vs. control) and
44 light levels (gap vs. closed forest).

45 3) Two out of the five species (hornbeam *Carpinus betulus* and lime *Tilia cordata*) were able
46 to develop a cage when exposed to ungulate herbivores, but only under high-light
47 conditions. These two species had the highest survival rates in the herbivory treatment over

48 a 10-year period. The expression of the cage architecture under high-light conditions only
49 indicates that this strategy incurs high costs and that trees face a strong trade-off between
50 tolerance to herbivore browsing and shade-tolerance.

51 *Synthesis.* Cage plasticity in temperate forest tree species may reflect an overlooked adaptation
52 to mammal herbivory (brown-world trait) originating in a past when large mammals exerted
53 strong selection pressures in European ecosystems. Our findings challenge the view of
54 closed canopy forest communities being solely driven by abiotic drivers and call for a re-
55 evaluation of the importance of large herbivores in shaping the functional traits of temperate
56 tree species.

57 Keywords: large herbivores, plant architecture, defence trait, forest structure, structural
58 defences

59 Introduction

60 The architecture of trees reflects both the main abiotic and biotic pressures under which trees
61 grew and evolved (Barthelemy & Caraglio 2007; Charles-Dominique *et al.* 2017; Kruger *et al.*
62 2017). Recent work from African wooded savannas suggests that we can divide woody plants
63 into architectural types, or functional trait syndromes, according to the main selection pressures
64 species are adapted to (Archibald & Bond 2003; Charles-Dominique *et al.* 2017; Charles-
65 Dominique *et al.* 2018). These main types have also been referred to as green, black and brown
66 world architectures (Bond 2005, Kruger *et al.* 2017). Green world trees combine a set of traits,
67 and resulting architecture that allow them to compete for abiotic resources. For example, long
68 internodes, large leaves and fast growth increase light capture and the capacity to reach the
69 canopy quickly under light-limited forest conditions (Dudley & Schmitt 1996; Dorn, Pyle &
70 Schmitt 2000; Dantas & Pausas 2013; Charles-Dominique *et al.* 2015a; Kruger *et al.* 2017;
71 Charles-Dominique *et al.* 2018, Fig. 1). Black world trees have architectures for withstanding
72 fires, including belowground perennial branches and thick bark that insulates their cambium
73 from heat damage (Dantas & Pausas 2013; Maurin *et al.* 2014; Charles-Dominique *et al.*
74 2015a). Lastly, brown world architectures, favoured in environments with high pressure from
75 mammalian browsers, usually correspond to densely branched trees with small stature, small
76 leaves and spines (Staver *et al.* 2012; Charles-Dominique *et al.* 2015b; Charles-Dominique *et*
77 *al.* 2017; Charles-Dominique *et al.* 2018, Fig. 1). While the plant morphological strategies for
78 green, brown and black worlds have recently been studied in savanna trees, it remains unclear
79 how much they matter elsewhere. Here, we ask to what extent saplings from temperate forests
80 have the ability to adjust their architecture in response to varying levels of light availability and
81 mammalian herbivory, *i.e.* whether they predominantly have a green or a brown architecture.
82 This study is among the first to investigate how the plasticity to induce a cage architecture

83 affects long-term survival of dominant temperate tree species in forest systems with abundant
84 large browsers.

85 Environmental drivers, such as light and herbivory, select for contrasting tree architectures. The
86 typical architecture found in light-limited environments (green world) consists of fast-growing,
87 elongated structures with large leaves facilitating access to and interception of light (Küppers
88 1989; Dudley & Schmitt 1996; Dorn, Pyle & Schmitt 2000; Charles-Dominique, Edelin &
89 Bouchard 2010; Charles-Dominique *et al.* 2012). In contrast, a cage architecture allows plants
90 to cope with mammalian herbivory by forming a dense, intricate, structure composed of a high
91 number of woody structural stems that restrict herbivore access to leaves and buds (Bond, Lee
92 & Craine 2004; Bond & Silander 2007; Staver *et al.* 2012; Charles-Dominique *et al.* 2017, Fig.
93 1). In systems with constant high densities of mammalian herbivores (brown world), such as
94 African savannas where the risk of herbivory is always high everywhere, one would expect
95 plants to evolve constitutive defences. Studies in these systems have shown that a plant's ability
96 to survive chronic herbivory depends largely on its ability to develop a cagy architecture
97 (Archibald & Bond 2003; Staver *et al.* 2012, Charles-Dominique *et al.* 2017).

98 In temperate forest systems, functional trait studies have traditionally focused on abiotic drivers,
99 especially light, as the main limiting factor determining tree architecture types (Kempf &
100 Pickett 1981; Kohyama 1987; Küppers 1989). However, large mammalian herbivores are an
101 integral component of temperate forests and a major driver of tree regeneration (Kuijper *et al.*
102 2010b; Laskurain *et al.* 2013; Forsyth *et al.* 2015), suggesting trees with cage architectures may
103 also be selected for in these systems. However, in these temperate forest systems herbivory
104 pressure is more variable in space and time than in many savanna systems. Moreover, high
105 herbivore pressure in forests is often associated with canopy gap formation, where increasing
106 light availability promotes tree regeneration (Runkle & Yetter 1987; Canham *et al.* 1990;
107 Bobiec 2007) but also mammalian browsing (Kuijper *et al.* 2009, Churski *et al.* 2017). Because

108 this gap formation is dynamic in space and time, plant species taking advantage of these gaps
109 are more likely to have evolved plastic architectures. High architectural plasticity enables
110 species to benefit from an elongated green architecture (Dudley & Schmitt 1996; Dorn, Pyle &
111 Schmitt 2000) when growing in a closed-canopy forest with limited light and relatively low
112 herbivory levels, but revert to a cagy brown world structure when forest gaps open, increasing
113 light and herbivore pressure. Moreover, high herbivory pressure and high light levels can also
114 be decoupled, e.g. in areas where predation risk from large carnivores locally reduces herbivore
115 densities (van Ginkel *et al.* 2019). When forest gaps open in such areas with low herbivore
116 pressure, an elongated, fast-growing green architecture can give trees a competitive advantage
117 for reaching the tree canopy more quickly than trees that maintain a cagy architecture. In other
118 words, more so than savanna trees, temperate forest tree species may benefit from an ability to
119 shift from a green to brown world architectural strategy. While induced defences (both chemical
120 and structural) have been well documented for insect herbivory (Karban, Agrawal & Mangel
121 1997; Gardner & Agrawal 2002; Van Bael, Brawn & Robinson 2003), we still know much less
122 about the induced architectural response to large mammalian herbivores. Moreover, we still
123 know little about the consequences of switching between different architecture types on the
124 survival of trees.

125 In this study, we investigated the plasticity of cage architecture in five European tree species
126 using a long-term field experiment during which we planted and grew 720 saplings of five
127 dominant European tree species for a 10-year period under varying levels of controlled
128 browsing and light availability. We specifically questioned whether these European tree species
129 were able to develop/induce a cage architecture and how this affected their long-term survival
130 in the face of browsing.

131 MATERIAL AND METHODS

132 *Study area*

133 The study was conducted in the Polish part of Białowieża Forest (BF, Fig. 2). BF (1450 km²),
134 situated in eastern Poland (600 km², 52°45' N, 23°50' E) and western Belarus (850 km²), is a
135 large continuous forest composed of multispecies tree stands. The present study was carried out
136 in the managed part of BF, where forestry and ungulate management occur (Fig. 2). The area
137 predominantly consists of forest (99.2% of the area), interspersed with forest gaps and narrow
138 river valleys. A mosaic of forest types is dominated by deciduous oak-lime-hornbeam stands
139 composed of pedunculate oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.) and
140 common hornbeam (*Carpinus betulus* L.). Five native ungulate species occur in the area, with
141 red deer (*Cervus elaphus*) being the dominant browsing ungulate (Bubnicki *et al.* 2019; Churski
142 *et al.* 2021). During an ungulate drive count in 2011, red deer density in the managed part of
143 BF was an estimated 4.7 individuals/km² (Borowik, Wawrzyniak & Jedrzejewska 2016). The
144 second-most numerous ungulate in those counts was the wild boar (*Sus scrofa*) – 3.2 ind./km²,
145 followed by roe deer *Capreolus capreolus* (0.8 ind./km²). The two largest species had the lowest
146 densities (<1 ind./km²) – the European bison (*Bison bonasus*) and moose (*Alces alces*). These
147 ungulates co-occur with their natural predators, the wolf (*Canis lupus*) and lynx (*Lynx lynx*),
148 which have been strictly protected since 1989. For more details about the study area see Churski
149 *et al.* (2017).

150

151 *Experimental design*

152 In 2008, we selected six forest gaps that had been clear-felled prior to the experiment's start.
153 These forest gaps differed in size between 236 and 2803 m² (median 736 m²) and represented
154 patches with high light availability (hereafter high-light). They were situated in tree stands
155 ranging from mixed deciduous (with dominant canopy species *Carpinus betulus* L., *Quercus*
156 *robur* L., *Tilia cordata* Mill.) to mixed coniferous (Norway spruce *Picea abies* (L.) H. Karst,
157 *Carpinus betulus*, *Quercus robur*). Inside each forest gap we selected two plots, 7×7 m each,
158 one of which was randomly assigned to the control (no fence) and the other to the enclosure

159 (with fence) treatment. The fences were erected in March-April 2008 and excluded all ungulate
160 species (roe deer, red deer, moose, bison and wild boar), but provided free access to small
161 (rodents) and medium-sized herbivores (hares). For each forest gap, we selected two additional
162 plots in the closed-canopy forest directly bordering it. These plots represented patches with low
163 light availability (hereafter low-light). Again, one plot was randomly assigned as a control and
164 one as an enclosure. Hence, at each of the six locations we created a set-up with four plots (24
165 plots in total) in a full-factorial design manipulating light availability (high-light, low-light) and
166 ungulate browsing (enclosure, control).

167 In April 2008, in each plot we planted tree saplings of the five most dominant tree
168 species in BF: *Q. robur*, *C. betulus*, *Acer platanoides* (Norway maple), *P. abies*, and *T. cordata*.
169 These five species were also present as common canopy trees in the vicinity of the plots. All
170 saplings originated from a local tree nursery that used locally collected seeds. All saplings were
171 in the height class 50-100 cm, but saplings of different species differed in age: one (*C. betulus*),
172 two (*A. platanoides*, *Q. robur*, *T. cordata*) and four years old (*P. abies*). We planted six
173 individuals of each species (30 tree saplings per plot) in an equally spaced grid covering the
174 plots, with a distance of ca. 50 cm between tree saplings (Fig. 2). To prevent clumping, each
175 row of saplings included all five species, and the order of each species varied between rows. In
176 total we planted 720 saplings (36 saplings per species per treatment), each individually marked
177 with a unique plastic tag. During earlier studies we estimated ungulate visit rate by means of
178 camera traps and track plots on these plots (Kuijper *et al.* 2009). For a more detailed description
179 of the experimental design and analysis of the growth response of the planted trees to the
180 experimental treatments see Churski *et al.* (2017).

181 *Sapling architecture measurements*

182 We counted the number of branches as the total number of dead and living stem apices at the
183 time of planting (April 2008) and two years after (September 2010), covering in total three

184 growing seasons. During those two sampling events, we also recorded browsing marks on every
185 counted branch to estimate ungulate browsing intensity per sapling. As a measure of cage
186 plasticity we divided the increase in the number of branches of a sapling by the final height of
187 that sapling. This measurement (relative branching density index, RBDI hereafter) was inspired
188 by Staver et al.'s (2012) branching density index and allowed us to contrast individuals that
189 grew tall with a given branching density (low RBDI values), with individuals of the same
190 branching density that stayed relatively short (high RBDI values). A higher RBDI reflects
191 higher cage plasticity. We calculated RBDI to show the increase in branching density per
192 sapling over time, taking into account the initial branching state:

$$193 \quad RBDI = \left(\frac{N_{final}}{N_{initial}} \right) / H_{final} \quad \text{eqn. 1,}$$

194 (N_{final} is the total number of branches of each individual sapling counted in the last year of the
195 experiment, $N_{initial}$ the number of branches counted in the first year, and H_{final} the height of each
196 individual sapling measured in the last year of the experiment). We calculated the RBDI as the
197 relative increase in branching density over the three growing seasons following the start of the
198 experiment (autumn 2010).

199 *Sapling survival after 10 years*

200 The plots were revisited in May-June 2018 to record the survival of each planted individual
201 (scored dead or alive). During this 10-year period we regularly checked and repaired the
202 exclosures when necessary. In two exclosure plots fallen trees destroyed part of the fencing,
203 giving deer temporary access to the plots. However, this damage occurred in the latter part of
204 the 10-year period and, despite low-level browsing on lateral branches, this did not affect tree
205 survival as saplings had already largely grown out of the reach of herbivores (>1.5 m on
206 average, see Supporting Information, Table S1). After the 10-years, the canopy gaps were still

207 clearly visible. We, therefore, expect that the contrasting light conditions between the forest gap
208 plots and the closed-canopy forest plots were strong and relatively stable throughout our whole
209 study period.

210 *Statistical analyses*

211 We used linear mixed effects models, as implemented in the R package ‘nlme’ (Pinheiro *et al.*
212 2015), to determine whether there were any initial inter-specific differences in height and
213 branching density among the treatments (Supporting Information Fig. S1, Tables S1-S3).

214 We analysed the RBDI with linear mixed effects models (Pinheiro *et al.* 2015) using herbivory
215 (binary), light (binary), tree species (five levels) and all possible two-way and three-way
216 interactions as fixed effects. To take into account the hierarchical design of the experiment, we
217 included nested random effects (site/light/herbivory) on the model’s intercept. We tested for
218 pairwise differences with Holm post hoc tests as implemented in the R package ‘phia’ v. 0.2-1
219 (De Rosario-Martinez, 2015). We ran these models for all data, and then reran the same models
220 using only the upper quartile of the RBDI values. We did this because previous work has
221 suggested that these “top performers”, i.e., those individuals that built an effective cage
222 structure most rapidly, may more accurately describe the ability of tree species to survive and
223 escape the browse-trap than average individuals (Wakeling, Staver & Bond 2011). The RBDI
224 values were normally distributed in each experimental treatment, and the model residuals, were
225 normally distributed (Figs. S2-S5).

226 We then ran linear mixed effects models to evaluate the effect of browsing intensity
227 on individual saplings on the RBDI. For this analysis, we only used the data from the control
228 plots, where browsing occurred, and combined high-light and low-light plots. We combined
229 these treatments to ensure sufficient sample size, because saplings in the control plots had
230 variable mortality rates (Table S4). Moreover, the browsing intensity was influenced by light
231 conditions (higher in high-light plots; Kuijper *et al.* 2009, Churski *et al.* 2017), but there was

232 also substantial variation in browsing intensity within light treatments (Fig. S6). Thus,
233 combining both treatments allowed us to focus our inference on the species-specific effects of
234 browsing intensity on RBDI, while controlling for any potential clustering effects by including
235 light condition as a random effect (Fig. S7). Instead of using browsing intensity as a continuous
236 variable, we categorized it into three levels: Low – 1st quartile, Medium – 2nd and 3rd quartiles,
237 and High – 4th quartile. We included browsing intensity, tree species (five levels), and their
238 interaction as fixed effects. Again we performed separate analyses for the entire sample
239 distribution and for the upper quartile of the RBDI value distribution.

240 Finally, we checked whether the relative branching density, which we measured after
241 the first three growing seasons, affected the survival of saplings ten years after the start of the
242 experiment (in 2018). We fitted a generalized linear mixed effects model with binomial
243 distribution (mixed effects logistic regression) to the survival data of all originally planted
244 saplings growing in the high-light control plots (i.e., exposed to browsing by herbivores for 10
245 years). We used only high-light control plots as no *A. platanooides*, *P. abies* and *Q. robur* saplings
246 survived in the low-light control plots. *T. cordata* and *C. betulus* survival under the latter
247 conditions was also low and below 15%. Moreover, by only using data from the high-light plots,
248 we assured that light was not a limiting factor for survival probability of saplings, thus
249 strengthening our inference on the effect of RBDI on sapling survival. We included two additive
250 random effects in the model, controlling for variation between the sites and species. We decided
251 to include species as a random effect as in this analysis we were primarily interested in
252 understanding the effect of RBDI (expressed as a trait common to all species under
253 consideration) on sapling survival and not in the mean differences in RBDI between species
254 *per se* (see Fig. S8 for model diagnostics).

255 Results

256 *Sapling height and branching density at the start of the experiment*

257 At the beginning of the experiment, trees had similar heights across all browsing and light
258 treatment plots (exclosure vs. control: $F_{1,11} = 0.267$; $P = 0.615$; high-light vs. low-light: $F_{1,5} =$
259 0.633 ; $P = 0.462$), but height did vary among species ($F_{4,692} = 239.506$; $P < 0.0001$, Tables S1-
260 S2). Likewise, trees had similar initial branching density across all the browsing and light
261 treatments (exclosure vs. control: $F_{1,11} = 1.953$; $P = 0.19$; high-light vs. low light: $F_{1,5} = 2.069$;
262 $P = 0.21$; Tables S2-S3), but branching density differed among species ($F_{4,692} = 728.613$; $P <$
263 0.0001 , Fig. S1). *P. abies* had the highest initial branching density, followed by *C. betulus*, *Q.*
264 *robur*, *T. cordata* and *A. platanoides*, Fig. S1, Table S2).

265

266 *Effects of herbivory and light on relative branching density (RBDI) after three years*

267 Overall, the mean relative branching density index (RBDI) differed significantly among species
268 ($F_{4,549} = 90.369$, $P < 0.0001$) and depended on light availability (Table 1, Fig. 3). Three species
269 (*C. betulus*, *T. cordata* and *A. platanoides*) significantly increased their numbers of branches in
270 the presence of herbivores. Among these, *C. betulus* showed the highest increase in RBDI,
271 followed by *T. cordata* and *A. platanoides*. The remaining two species (*Q. robur* and *P. abies*)
272 showed the lowest mean relative increase in their numbers of branches, indicating low or no
273 cage inducibility under our experimental conditions (see Table 2 and Fig. 3 for effect sizes, and
274 Table S5 for post-hoc χ^2 test parameters and P -values).

275 The variation in RBDI between treatments (when analysing the entire distribution of
276 samples) was highly species-dependent (herbivory \times light \times species: $F_{4,549} = 4.371$, $P = 0.0017$,
277 Table 1, Fig. 3). In high-light conditions, *C. betulus* and *T. cordata* saplings produced
278 significantly more branches in the presence of herbivores than in the exclosures, whereas in
279 low-light there was no difference. *A. platanoides* was the only species that increased the number
280 of branches in the presence of herbivores, both in the high light and low-light plots. However,
281 in absolute terms, it had the lowest branching density of all species (Fig. 3, Table S2). *P. abies*

282 had significantly lower RBDI in the controls than in the exclosures, but only in the high-light
283 plots. The RBDI of *Q. robur* did not differ between the exclosure and control plots in either the
284 high-light or low-light conditions (Fig. 3, Tables 2, S2 and S5). Qualitatively, when analysing
285 just the upper quartile of the distribution of samples, the results were the same (Fig. 3, Table 1).

286 Browsing intensity affected RBDI in the same way for all species when analysing the
287 entire distribution of samples (although there was a non-significant interaction between
288 browsing intensity and species, Fig. 4, Tables S6 and S7). However, when analysing the top
289 25% RBDI of the saplings (the 4th quartile), the effect of browsing intensity varied among
290 species (significant interaction, Table 3, Fig. 4). For individuals in the 4th quartile, RBDI was
291 highest in *C. betulus* at medium levels of browsing intensity (RBDI = 0.7 ± 0.03 , Table 4) and
292 significantly higher than at low (RBDI = 0.46, $\chi^2 = 17.757$, $P < 0.001$) and high (RBDI = 0.34,
293 $\chi^2 = 39.676$, $P < 0.001$) levels of browsing intensity. For *T. cordata* and *A. platanoides*, RBDI
294 did not differ between different levels of browsing intensity. Whereas, both *Q. robur* and *P.*
295 *abies* showed small (compared to *C. betulus*) but significant differences between different levels
296 of browsing intensity ($\chi^2 = 10.288$, $P = 0.015$ and $\chi^2 = 37.394$, $P < 0.001$, respectively; for the
297 post-hoc χ^2 and P values see Table S8). Noteworthy, in contrast to *C. betulus*, RBDI for *Q. robur*
298 and *P. abies* was highest under low browsing intensity. Compared to all other species, *P. abies*
299 individuals in the 4th quartile had the lowest RBDI at each level of browsing intensity.

300 *Survival after 10 years in relation to branching plasticity*

301 Ten years after the start of the experiment, in high light plots in the presence of herbivores, the
302 best surviving species (*T. cordata* and *C. betulus*) had the highest average RBDI values (Figs.
303 5 and 6). The survival probability 10 years after the start of the experiment showed that an
304 individual's survival strongly increased with increasing RBDI (Fig. 5, RBDI = 2.49, SE = 1.36,
305 $z = 1.826$, $P = 0.068$, Table S9).

306

307 Discussion

308 Of the five dominant European temperate forest species we studied (*A. platanoides*, *C. betulus*,
309 *P. abies*, *Q. robur*, *T. cordata*), two (*C. betulus*, *T. cordata*) developed an effective cage
310 architecture that was associated with increased survival after 10 years. Interestingly, these
311 species only developed a cage architecture while growing in high-light conditions in forest
312 canopy gaps, indicating that a cage architecture is costly and can only be produced in resource-
313 rich conditions. These species also displayed plasticity as they switched between a brown
314 world, cage architecture under conditions of high light and browsing, and a green world, more
315 elongated architecture under conditions of high light without browsing (Fig. 6). Species with
316 low cage plasticity were eliminated from the plots exposed to herbivory within 10 years after
317 the start of the experiment. We discuss below that cage plasticity is an overlooked adaptation,
318 a brown-world trait, of temperate forest tree species.

319

320 *Relative Branching Density Index versus Branching Density Index*

321 Indices such as branching density index (BDI, Staver *et al.* 2012; Perez-Harguindeguy *et al.*
322 2013) or Investment in Structural Defences (ISD, Charles-Dominique *et al.* 2017) can be used
323 to identify species with constitutive defences. However, in systems with highly variable
324 browsing intensity, relative indices, such as our Relative Branching Density Index (hereafter
325 RBDI), may be more suitable for capturing the plasticity of cage architecture. In our study, the
326 absolute branching index did not capture this plasticity well, and it was crucial to include
327 information on initial branching density. For example, coniferous *P. abies* saplings had the
328 highest initial branching density compared to the other species. Coniferous species have a
329 different constitutive architecture and ontogenesis compared with deciduous species, which
330 may explain this initial difference (e.g., Bond 1989; Romberger, Hejnowicz & Hill 1993).
331 However, it was also the only species for which branching decreased in response to ungulate

332 browsing. After correcting for the initial number of branches (our RBDI), *P. abies* had the
333 lowest relative increase in branching, and RBDI was lower with browsing than without.
334 Importantly, when in the presence of ungulates, this lack of response to chronic browsing was
335 associated with the species having the lowest survival after 10 years.

336

337 *RBDI as a brown world trait in temperate forests*

338 High branching density is an important trait helping trees to escape from or defend against
339 herbivores in environments driven by large herbivores such as African savannas (Archibald &
340 Bond 2003; Bond 2005; Fornara & Du Toit 2007; Staver *et al.* 2012; Charles-Dominique *et al.*
341 2017). To our knowledge our study is the first to show that intense branching, resulting in a
342 cage-like architecture, is also associated with increased survival in temperate forest trees. At
343 the species-level and in plots exposed to browsing, survival after 10 years was much higher for
344 species with high relative (RBDI) and absolute branching density. Moreover, at the individual
345 level, sapling survival greatly increased with increasing RBDI. These results suggest that cage
346 plasticity, expressed as RBDI, is an important defence trait in temperate forest systems and
347 increases plant fitness in the presence of large mammalian herbivores. In line with this,
348 Cromsigt & Kuijper (2011) previously described how intense browsing of regenerating saplings
349 in canopy gaps in BF creates and maintains patches of tree saplings in a lawn-like state. *C.*
350 *betulus*, the species with the highest cage plasticity in our study, dominates these browsing
351 lawns. In other studies in BF, we have shown in both long-term enclosure (Kuijper *et al.* 2010a,
352 Churski *et al.* 2017) and observational studies (Kuijper *et al.* 2010b) that chronic ungulate
353 browsing promotes the dominance of this tree species. Therefore, we interpret cage plasticity
354 to be a brown-world trait (Bond 2005) granting tree saplings a competitive advantage in
355 resource rich, consumer-controlled forests (Churski *et al.* 2017). Species unable to develop a

356 cage architecture (low cage plasticity) were eliminated from the plots exposed to herbivory
357 within 10 years of the start of the experiment.

358

359 *Trade-offs between browsing and shade tolerance*

360 In herbivore-dominated savannas, the development of a cagey architecture as a defence against
361 browsing has been described as a constitutive trait with little plasticity (Charles-Dominique *et*
362 *al.* 2017). In savannas, it makes sense for plants to have a high level of constitutive defence, as
363 mammalian herbivory is often omnipresent, and light availability generally does not limit tree
364 recruitment due to the relatively open tree canopies. In fact, constitutively cagey plants (low
365 cage plasticity) are generally eliminated from shaded environments (Ratnam *et al.* 2011;
366 Charles-Dominique *et al.* 2015; Charles-Dominique *et al.* 2018). However, we suggest that cage
367 plasticity is a highly desirable trait in closed-canopy forest systems with gap dynamics, with
368 variable light levels that can strongly interact with herbivory. This may be particularly true in
369 old-growth forests (Runkle 1981; Bobiec *et al.* 2000), and in our previous work we showed that
370 increased light availability in forest gaps facilitates recruitment of trees but also attracts intense
371 browsing (Kuijper *et al.* 2009, Churski *et al.* 2017). Our results indicate that, in contrast to
372 savanna trees, intermediate, and highly variable, light and herbivory conditions in temperate
373 forests have selected for trees with high architectural plasticity that can adjust their response to
374 strongly opposing selection pressures (herbivory and shade). In our forest gaps, species with a
375 high cage plasticity (*C. betulus*, *T. cordata*) outperformed the less plastic species (*P. abies*, *A.*
376 *platanoides* and *Q. robur*) in terms of survival and height increment (see Table S10, Figs. S9-
377 S10) after a 10-year period in plots with herbivores. In contrast, the less plastic species
378 performed better inside the exclosures (in comparison to browsed control plots) either under
379 high (*P. abies*, *Q. robur*) or low-light conditions (e.g. *A. platanoides*, Table S10, Figs. S9-S10).
380 *A. platanoides*, as a shade-tolerant specialist (largest height increment and survival in low-light

381 enclosure plots, Table S10), with a ‘green-world’ pole-like architecture (Fig. 1 and 6), was
382 unable to form a cage and eliminated from plots with herbivores present. Our results, therefore,
383 indicate that persistence of tree saplings at low light levels (under a closed tree canopy) requires
384 different architectural traits than persistence at high levels of browsing, suggesting a trade-off
385 between tolerance to high herbivory and tolerance to shade. The extent to which plants can
386 induce plastic responses is determined by physiological constraints in their allocation of carbon
387 (Herms & Mattson 1992; Diaz *et al.* 2016). The species with the strongest architectural
388 plasticity, *C. betulus* and *T. cordata*, developed clear cage architectures after ten years of intense
389 browsing, but only under high-light conditions (canopy gaps) and, in *C. betulus*, under
390 intermediate herbivory levels (Fig. 4). The low survival and height increment we observed
391 under low-light and high-herbivory suggest tree saplings may be unable to create a cagey
392 architecture under these circumstances because they cannot compensate for lost phytomass with
393 regrowth (Table S10).

394 Since light levels and herbivory are highly variable in old-growth temperate forests (Kuijper *et*
395 *al.* 2009; Churski *et al.* 2017), the mixed green-brown world strategy shown by *C. betulus* and
396 *T. cordata* allows these species to induce a cage architecture when exposed to herbivory, but
397 go for fast vertical growth in its absence. This fast vertical growth allows plants to reach the
398 forest canopy, which drastically increases the resources available to the plant and frequently
399 triggers reproduction in these species. Trees with suppressed growth, either due to shade or high
400 herbivory, can stay in a non-reproductive state for long periods (Archibald & Bond 2003). We
401 argue that the ability to form a cage architecture enables trees to tolerate high levels of chronic
402 browsing while still allowing them to slowly increase in height (Table S10, Figs. S9-S10). In
403 this scenario, the cage architecture likely protects stems and buds inside the cage from
404 browsing, or reduces the overall browsing intensity per individual shoot (i.e. ‘safety in numbers’
405 or ‘dilution effect’). In the long-term the ability to increase in size and height will allow a tree

406 to outgrow the reach of browsing ungulates (see Kuijper *et al.* 2013) and hence escape the
407 browse trap (Cromsigt & Kuijper 2011; Staver & Bond 2014, Churski *et al.* 2017). Escape from
408 the browse trap may also be enhanced when the cage is large enough to physically block
409 ungulates from reaching the inside of the cage, where shoots can escape ('hedge effect', see
410 Fig. 7). In BF, species with the highest cage plasticity (i.e., *C. betulus* and *T. cordata*) can often
411 be observed as cone-shaped trees, indicating their escape from herbivore browsing after having
412 formed a cage architecture (Fig. 7).

413

414 *Considering cage plasticity as an ecological anachronism*

415 Several authors have used the concept of ecological anachronisms to explain plants having re-
416 dundant defence traits in systems where the large megafaunal browsers that selected for those
417 traits are extinct. Certain Madagascan tree species, for example, still develop a divaricate archi-
418 tecture that likely deterred the now extinct Moas (Bond & Silander 2007). Similarly, we spec-
419 ulate that the architectural plasticity of dominant temperate species suggests megafauna had a
420 strong effect on ecosystems in Europe (see Sandom *et al.* 2014) and conflicts with the "high-
421 forest hypothesis" that suggests large mammals played a limited role during the Holocene
422 (Birks 2005).

423 In this context, it is noteworthy that the constitutive expression of a cage architecture, which is
424 very common in savanna systems, is also present among common temperate European species
425 such as *Crataegus monogyna*, *Prunus spinosa*, and *Rosa canina* (Vera 2000). There are three
426 components involved in building a constitutive cage architecture: high number of axis catego-
427 ries contributing to the cage, stem woodiness, and spinescence. The best protection against
428 browsing herbivores is achieved by species having both spines and a high number of axis cate-
429 gories contributing to the cage (Charles-Dominique *et al.* 2017). The developmental costs of
430 these structural defences, however, are very high (Charles-Dominique *et al.* 2017). As a result,

431 species with a constitutive cage architecture are uncompetitive and occur infrequently in shaded
432 environments such as closed-canopy forests (Kruger *et al.* 2017). Since a constitutive cage ar-
433 chitecture is costly, such plants require open landscapes, i.e. unlimited light resources. Within
434 present-day Europe, we observe these species around fields or along forest edges in extensively
435 used agricultural land or wood-pastures (Smit & Ruifrok 2011; Cornelissen *et al.* 2014). How-
436 ever, rather than reflecting a dependence on human land use that opens up forests, the cage
437 architecture of these species may be an ecological anachronism originating in a megafauna-
438 dominated past. Our results confirm that a cage-architecture strongly increases plant survival
439 under intense chronic browsing. Screening European woody flora for constitutive and induced
440 cage architecture could contribute towards further revealing the impacts of (extinct) megafauna
441 on plant evolution and European vegetation structure. This, in turn, is likely to inform wide-
442 spread initiatives to restore trophic complexity and top-down control of vegetation in European
443 ecosystems, e.g. through trophic rewilding.

444

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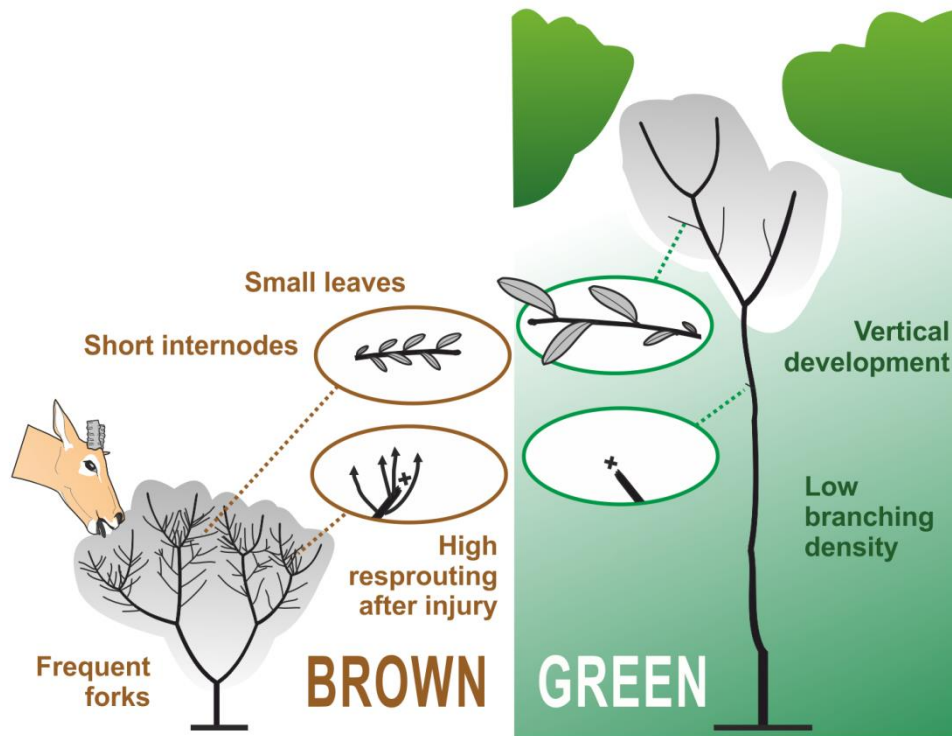
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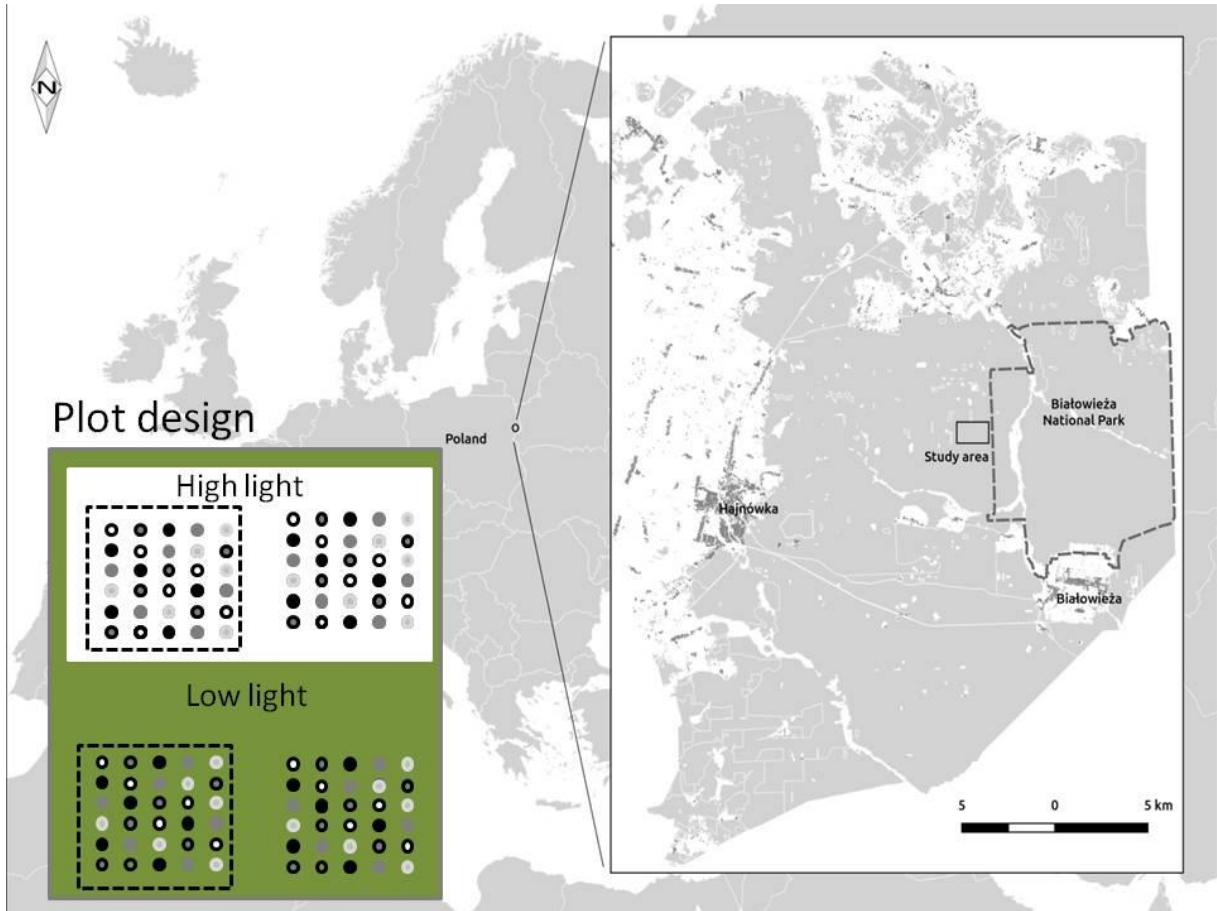
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600 Fig. 1. Conceptual illustration of woody plant architectural types and associated traits. Trees
601 with typical green world traits (*sensu* Bond 2005, Kruger *et al.* 2017) have an architecture
602 maximizing resource (e.g. light) acquisition: internode elongation, large leaves and fast
603 growth to reach the canopy level quickly under light-limited forest conditions. In contrast,
604 trees with brown world architectures, to cope with high pressure from mammalian browsers,
605 are typically densely branched with small stature, small leaves and spines.

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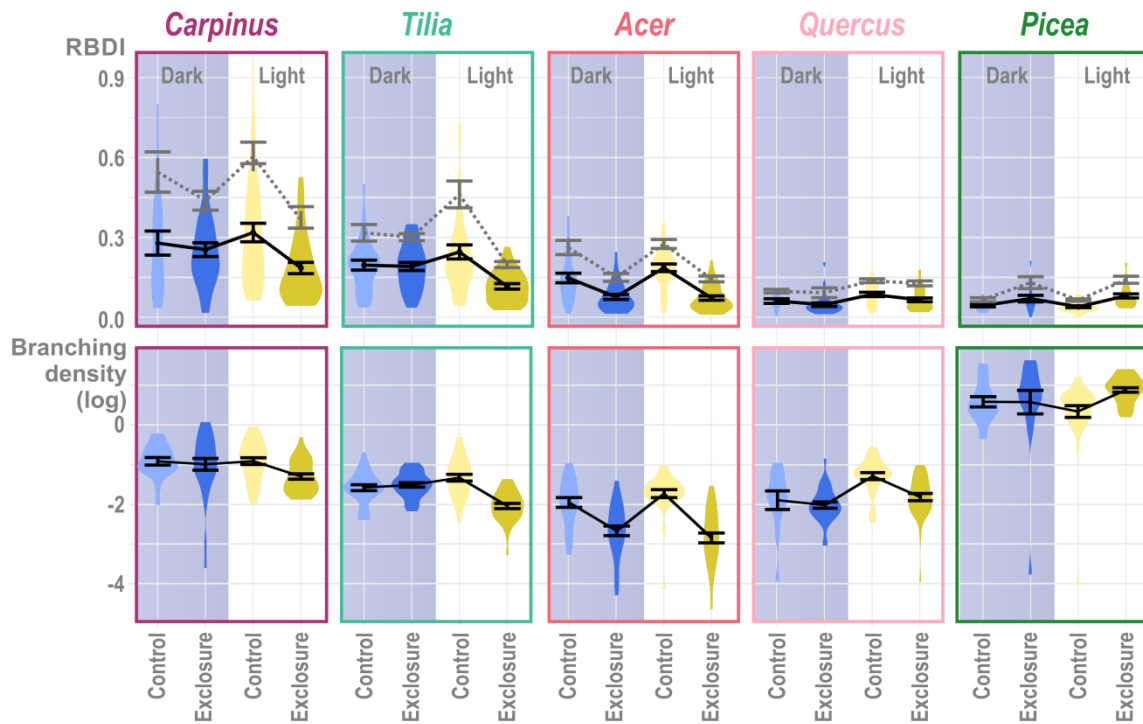


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609 Fig. 2. Study area and experimental plot design. At each of six locations we established four
610 plots, two of which were in a forest gap (high light treatment) and two under the canopy (low
611 light). Each light treatment received both an exclosure (dashed lines) and a control (no line)
612 plot. At each plot six saplings each of five species were planted (marked with different circles)
613 with random placement. This setup was replicated six times.

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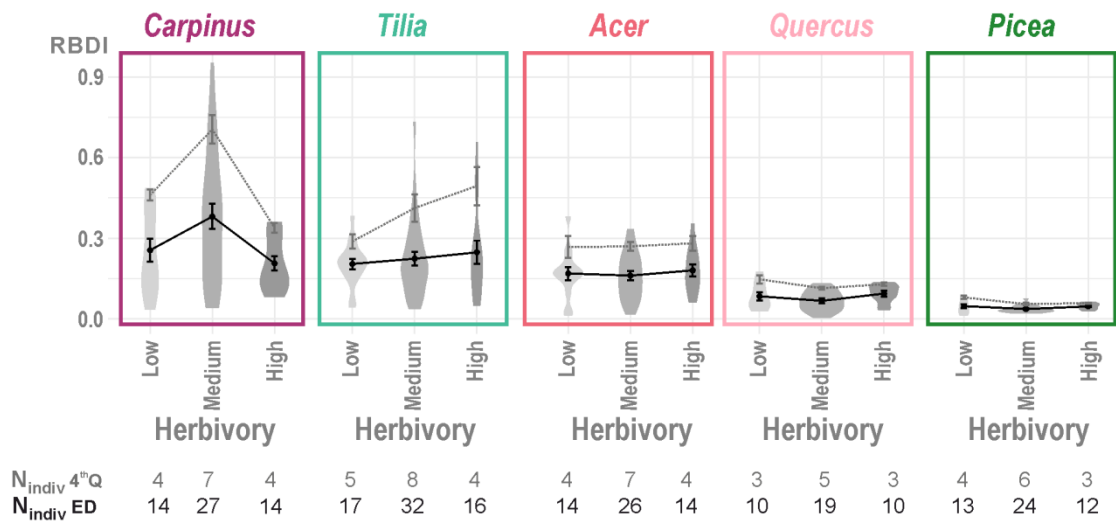


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617 Fig. 3. Relative branching density index (RBDI, top panel) and branching density (log scale,
 618 bottom panel) of each planted species in the control and exclosure and in the high light (light)
 619 and low light (dark) treatments. The black solid line indicates the mean values (+/- SE) of RBDI
 620 and Branching density for the entire distribution of samples, and the dotted line the mean values
 621 (+/- SE) for the upper (4th) quartile only (“best individuals”). The colour palette used is colour-
 622 blind friendly.

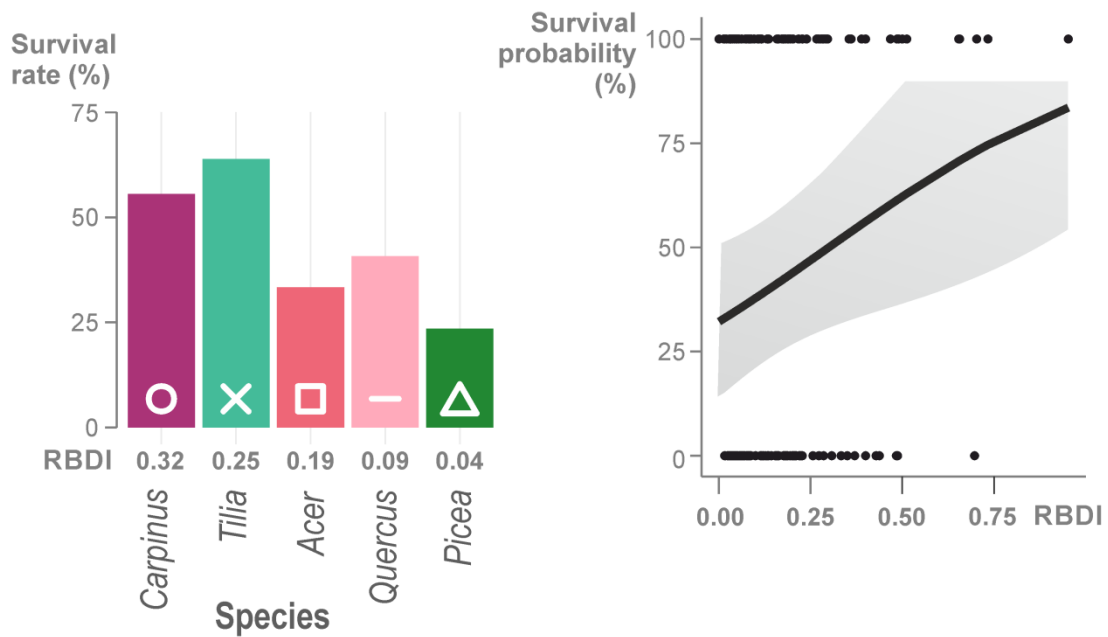
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 626 Fig. 4. Relative branching density index (RBDI) of each planted species in the control plots and
 627 in the different levels of browsing intensity (low, medium and high). The browsing pressure
 628 (originally a continuous variable indicating the percentage of browsed stems in the total number
 629 of stems) was categorized into three levels: Low – 1st quartile, Medium – 2nd and 3rd quartiles,
 630 High – 4th quartile. The black solid lines indicate the mean values (+/- SE) of RBDI for the
 631 entire distribution of samples, and the dotted lines the mean values (+/- SE) for the upper (4th)
 632 quartile only (“best individuals”). The numbers below each category indicate the numbers of
 633 individuals. Colour palette used is colour-blind friendly.

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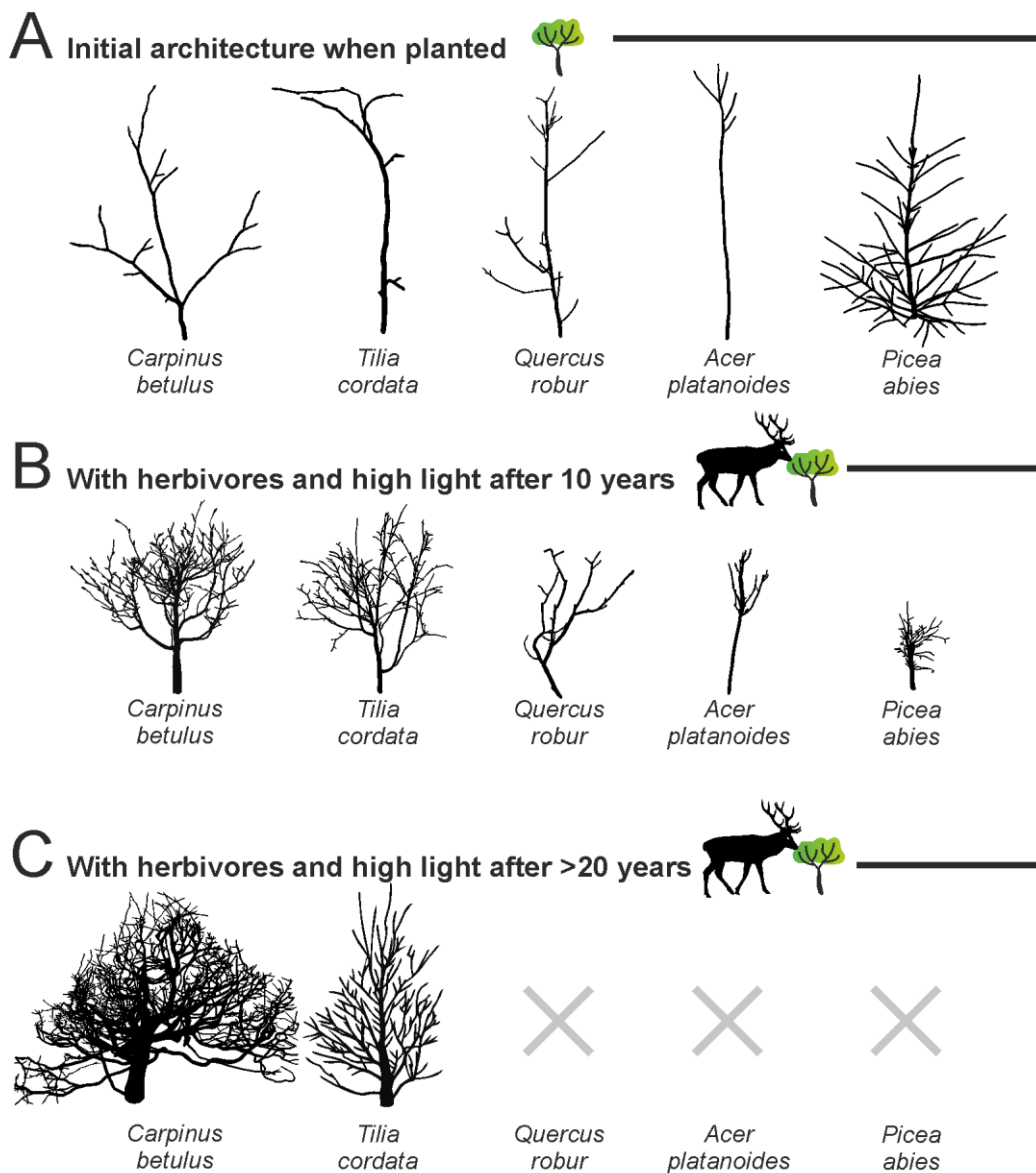
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636 Fig. 5. Probability of the planted saplings surviving 10 years after the start of the experiment.
 637 Left panel shows the proportion of saplings that survived per species, with the adjusted mean
 638 (based on the model) relative branching density index (RBDI) below the bars. Right panel
 639 shows predicted survival probability (10 years after the start of the experiment) from a logistic
 640 regression model of individually tagged saplings, independent of species, in relation to the
 641 individuals' RBDI value that we measured two years after the start of the experiment. Only
 642 saplings planted in control and high light treatments were used in this analysis. Colour palette
 643 used is colour-blind friendly.

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648 Fig. 6. Visualization of typical examples of measured architectures of tree saplings belonging to the five species used in our experiment at the start (A) and after 10 years B). In panel C we
 649 show the projected architectures based on long-term exclosure studies in our system (Churski
 650 et al. 2017, Kuijper et al. 2010) in combination with the species-specific survival rates presented
 651 in the current study. The tree architectures shown in (C) are based on observed architectures in
 652 old forest gaps (at least 20 years old), where heavily pruned and cage-like individuals of *C.*
 653 *betulus* and *T. cordata* dominate and other species are largely absent (Cromsigt et al. 2011). All
 654 architectures are drawn from photos of typical individuals.

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663 Fig. 7. *Carpinus betulus* in two commonly observed stages of its development in Białowieża
664 Forest: strongly suppressed individuals under intense ungulate browsing form a dense cage
665 architecture (left) that allows them to escape herbivore control when top-shoots grow out of
666 reach of browsing herbivores (right).

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669 **Table 1** Analysis of deviance table based on the linear mixed-effect model estimated for both
 670 the entire distribution and the upper quartile of samples explaining the variation in the relative
 671 branching density index (RBDI) of the planted tree saplings in relation to the treatments
 672 (herbivory, light), species and their interactions.

Factor	Group DF	DF	F	<i>P</i>
<i>Entire distribution model</i>				
Intercept	1	549	537.6	<0.01
Herbivory	1	10	2.8	0.13
Light	1	5	0.05	0.84
Species	4	549	90.37	<0.01
Herbivory : Light	1	10	0.05	0.83
Herbivory : Species	4	549	28.41	<0.01
Light : Species	4	549	1.54	0.19
Herbivory : Light : Species	4	549	4.37	0.0017
<i>Upper quartile model</i>				
Intercept	1	110	1138.27	<0.01
Herbivory	1	10	1.67	0.22
Light	1	5	1.68	0.25
Species	4	110	105.38	<0.01
Herbivory : Light	1	10	0.04	0.84
Herbivory : Species	4	110	33.23	<0.01
Light : Species	4	110	1.8	0.13
Herbivory : Light : Species	4	110	3.37	0.012

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674 **Table 2** Adjusted mean RBDI values (based on the model) per species and treatment. Species
 675 are sorted according to RBDI values from highest to lowest within each treatment.

Light	Herbivory	Species	Adjusted mean RBDI	Standard error	
Low light	Control	<i>Carpinus</i>	0.28	0.04	677
	Control	<i>Tilia</i>	0.20	0.02	678
	Control	<i>Acer</i>	0.15	0.01	679
	Control	<i>Quercus</i>	0.06	0.01	680
	Control	<i>Picea</i>	0.04	0.01	681
	Exclosure	<i>Carpinus</i>	0.26	0.03	682
	Exclosure	<i>Tilia</i>	0.19	0.02	683
	Exclosure	<i>Acer</i>	0.08	0.01	684
	Exclosure	<i>Picea</i>	0.07	0.01	685
	Exclosure	<i>Quercus</i>	0.05	0.01	686
High light	Control	<i>Carpinus</i>	0.32	0.03	687
	Control	<i>Tilia</i>	0.25	0.02	688
	Control	<i>Acer</i>	0.19	0.01	689
	Control	<i>Quercus</i>	0.09	0.01	690
	Control	<i>Picea</i>	0.04	0.01	691
	Exclosure	<i>Carpinus</i>	0.19	0.03	692
	Exclosure	<i>Tilia</i>	0.12	0.02	693
	Exclosure	<i>Picea</i>	0.08	0.01	694
	Exclosure	<i>Acer</i>	0.07	0.01	695
	Exclosure	<i>Quercus</i>	0.07	0.01	696

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693 **Table 3** Analysis of deviance table based on the linear mixed-effect model explaining the
 694 relationship between the estimated mean relative branching density index (RBDI) for both the
 695 entire distribution and the upper quartile of samples and the browsing intensity.

Factor	Group DF	DF	F	P
<i>Entire distribution model</i>				
Intercept	1	236	340.04	<0.01
Species	4	236	79.88	<0.01
Browsing intensity category	2	236	3.46	0.033
Species : browsing intensity category	8	236	1.54	0.143
<i>Upper quartile model</i>				
Intercept	1	43	1518.25	<0.01
Species	4	43	172.39	<0.01
Browsing intensity category	2	43	16.32	<0.01
Species : browsing intensity category	8	43	5.57	<0.01

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697 **Table 4** Adjusted mean RBDI values per species and browsing intensity category calculated
 698 from individuals in the 4th RBDI quartile.

Species	Browsing category	Adjusted mean RBDI	Standard error
<i>Carpinus</i>	Low	0.46	0.05
<i>Tilia</i>	Low	0.30	0.06
<i>Acer</i>	Low	0.27	0.03
<i>Quercus</i>	Low	0.15	0.01
<i>Picea</i>	Low	0.09	0.00
<i>Carpinus</i>	Medium	0.71	0.04
<i>Tilia</i>	Medium	0.41	0.04
<i>Acer</i>	Medium	0.27	0.02
<i>Quercus</i>	Medium	0.11	0.01
<i>Picea</i>	Medium	0.06	0.00
<i>Tilia</i>	High	0.49	0.06
<i>Carpinus</i>	High	0.34	0.05
<i>Acer</i>	High	0.28	0.03
<i>Quercus</i>	High	0.13	0.01
<i>Picea</i>	High	0.06	0.00

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