

1 **Junipers enable heavily browsed rowan saplings to** 2 **escape ungulates in boreal forest**

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12 **Highlights**

- 13 • Abundance of rowan saplings increased excessively in old growth boreal forest when
14 excluding ungulates or when herbivore density decreased.
- 15 • Rowan growth was clearly limited by ungulate browsing, and saplings were not able
16 to escape the “browse trap” by growing beyond ca. half a meter.
- 17 • Rowan saplings established in juniper nurse plants were protected against browsing
18 and showed reduced mortality and increased growth.
- 19 • Our study showed that nurse plants enabled saplings to escape from feeding ungulates
20 in boreal forest.

21 Abstract

22 Recent increases in ungulate herbivore populations have intensified browsing pressure in
23 northern forest ecosystems. High browsing pressure affects recruitment into tree populations
24 and saplings are among the most impacted and critical tree stages. This calls for research on
25 factors that enhance sapling survival and promote recovery of herbivore preferred species.
26 One understudied factor in ungulate dominated boreal forests is the ability of young trees to
27 escape large herbivores by utilising “nurse plants”. First, we examined the impact of ungulate
28 browsing on the abundance and size of rowan (*Sorbus aucuparia*), a functionally important
29 tree species in an old-growth boreal pine forest, western Norway. The responses were
30 compared between exclosures and ungulate-access plots over ten years (2001–2011)
31 combined with investigations along a browsing intensity gradient (Exp. A). In a second
32 experiment we investigated whether rowan saplings escape browsing and enhance growth and
33 survival by growing within nurse plants. Consequently, we planted rowan saplings in ungulate
34 browsing areas, inside and outside coniferous juniper (*Juniper communis*) bushes, and
35 analysed the treatment effect on browsing, growth, and survival of rowan saplings across five
36 years (2013–2018; Exp B). Excluding large herbivores resulted in a large increase in rowan
37 saplings which were six times more abundant in exclosures (0.44 ind./m²) compared to
38 ungulate-access plots (0.07 ind./m²) after ten years (Exp. A). The abundance of rowan
39 saplings also decreased with higher browsing intensity. Moreover, the rowans in exclosures
40 grew to almost twice the height of the ungulate-access rowans. The protected rowan saplings
41 experienced significantly less browsing damage, and only 25% of the protected plants
42 experienced heavy browsing or died after the first winter, compared to 70% of the unprotected
43 plants (Exp. B). After five years, 50% more unprotected than protected plants experienced
44 heavy browsing or mortality, and growth in protected plants was nearly 50% greater over the
45 period. The negative impact of ungulate browsing on abundance and growth of rowans can be

46 counteracted by positive plant-plant interactions. Rowan saplings growing within nurse plants
47 showed significantly less browsing and better performance indicating high functional
48 importance of the forest understorey. Forest managed with multi-layered and multi-species
49 understoreys may therefore also be beneficial for tree recruitment in browsed boreal forest
50 landscapes.

51

52 **Keywords:** exclosures, facilitation, plant-plant interactions, plant-herbivore interactions,
53 mixed-species forestry, nurse plant, recruitment failure, rewilding, ungulate browsing

54 1. Introduction

55 Wild ungulate populations in Europe and North America have transformed from historical
56 minimum levels a century ago to an all-time high in the last couple of decades (Putman et al.,
57 2011; Speed et al., 2019). In northern forest ecosystems, this increased ungulate density is
58 now one of the main drivers of shifts in tree species composition at local scales (Skarpe &
59 Hester, 2008; Churski et al., 2017; Ramirez et al., 2018). For example, selective browsing
60 from species such as moose (*Alces alces*), red deer (*Cervus elaphus*), and white-tailed deer
61 (*Odocoileus virginianus*) may have benefitted conifers at the expense of deciduous tree
62 species in many forests (McInnes et al., 1992; Winnie, 2012). Selective browsing by large
63 herbivores on trees in young stages is of particular concern for forest managers as it exerts a
64 strong impact on tree populations through reduced growth and possible recruitment failure
65 (Kuijper et al., 2010; Speed et al., 2013; Lilleeng et al., 2016). In addition, domestic ungulates
66 may impact forest systems substantially (Laskurain et al., 2013; Hjeljord et al., 2014), and
67 globally, livestock has at least ten times the biomass of wild large herbivores (Ripple et al.,
68 2015).

69
70 Tree recruitment and growth are of fundamental importance in forest ecosystems, often
71 determining forest structure, species composition, and ecological functioning (Danell et al.,
72 2003; Hidding et al., 2013; Nuttle et al., 2014). However, tree saplings are often highly
73 palatable to both wild and domestic ungulates and need to avoid browsing to have a chance of
74 reaching maturity (Skarpe & Hester, 2008; Milne-Rostkowska et al., 2020). Indeed, young
75 stages such as seedlings and saplings are the most heavily impacted by large herbivores in
76 temperate and boreal forest (Bernes et al., 2018). In addition to physical and chemical defence
77 mechanisms, saplings can gain protection from herbivores when growing adjacent to less
78 preferred plants; a facilitation mechanism termed “the nurse-plant effect” or associational

79 resistance (Callaway, 1995; Filazzola & Lortie, 2014). Studies have shown that the likelihood
80 of herbivore-preferred sapling species being browsed by ungulates is often significantly lower
81 when they grow in association with less attractive, or better defended, species (Bee et al.,
82 2009; Harmer et al., 2010; Jensen et al., 2012). Exploitation of this nurse-plant effect is,
83 therefore, a potentially important management tool, particularly since the recovery of large
84 herbivore-preferred tree species may be very slow (D. Kuijper et al., 2010; Tanentzap et al.,
85 2012; Milne-Rostkowska et al., 2020). However, further research is required to understand the
86 field conditions under which species associations are likely to result in significant
87 performance and fitness gains for target species.

88

89 Facilitation among species, such as positive plant-plant interactions, is considered to be one of
90 the universal drivers of biodiversity (McIntire & Fajardo, 2014). Previous studies of
91 facilitative plant-plant interactions have often found them to be more common in stressful
92 environments (Bertness & Callaway, 1994; Callaway, 1995; Brooker et al., 2008), but there is
93 now increasing evidence that beneficial interactions are also common in moderately stressful
94 or productive environments (Holmgren & Scheffer, 2010; Bråthen & Lortie, 2016).

95 Consequently, the nurse-plant effect may provide an efficient management tool in mixed-
96 species forestry as nurse plants may both outcompete competitive field-layer vegetation and
97 protect target tree species from consumption (Löp et al., 2014; Löf et al., 2018). A review by
98 Filazzola and Lortie (2014) found few nurse-plant studies conducted in late successional
99 ecosystems with low levels of abiotic stress. Boreal forests, dominated by conifers, are
100 particularly underrepresented (see Bannister et al., 2020 as one of few examples), and
101 relatively few studies focus on sapling protection from large herbivores. Another potential
102 barrier to apply nurse plants as a management tool is that many experimental studies are
103 rather short-term. Therefore, we often cannot establish if positive interactions are transient or

104 persistent, and whether they may positively affect survival and growth in addition to reduced
105 browsing damage (Brooker et al., 2006; Brooker et al., 2008). As such there is need for more
106 research on facilitative plant-plant interactions and their direct effect on probabilities for
107 young trees in critical stages to escape large herbivore browsing, as well as long-term
108 consequences for the abundance and distribution of species and their usefulness to
109 management of biodiversity and restoration of ecosystems (Gomez-Aparicio et al., 2004;
110 Gomez-Aparicio, 2009; L f et al., 2018).

111

112 The current study addresses several of these research needs, focusing on rowan, *Sorbus*
113 *aucuparia*, as the target tree species and juniper, *Juniperus communis*, as the nurse plant in a
114 boreal forest in Norway. Rowan is considered a functionally important species in northern
115 forests as it is one of the most attractive food trees for ungulate browsers (Mysterud et al.,
116 2010; Milne-Rostkowska et al., 2020), it is one of few abundant flowering resources for
117 pollinators during spring (Mayer et al., 2012) and it provides extensive berry supplies to birds
118 and mammals before and during winter (Paulsen & H gstedt, 2002). In Norway, rowan is
119 monitored in the national forest inventory to estimate spatial and temporal variation in
120 browsing pressure (Solberg et al., 2012), as it is recognised that browsing may significantly
121 affect rowan population structure and reduce local abundance (Speed et al., 2013; Hegland &
122 Rydgren, 2016). Browsing has a clear negative effect on rowan transition rates from small to
123 medium size classes (Edenius & Ericsson, 2015), and adult reproducing rowans are often rare
124 in browsed forest ecosystems (Myking et al., 2013). Ungulates may browse repeatedly on
125 individual rowan trees, resulting in low statured trees forming fine-scaled browsing lawns
126 within forested areas (Speed et al., 2013).

127

128 In previous work at our study site in old growth pine forest at Svanøy, western Norway, we
129 have observed that small juvenile rowan sometimes grows within the dwarf-shrub bilberry
130 (*Vaccinium myrtillus*) and within bushes of the coniferous juniper. Juniper is a rather large
131 understory shrub co-occurring with rowan throughout Europe and is largely unfavoured by
132 ungulates (Miller et al., 1982; Raspe et al., 2000; Thomas et al., 2007). Junipers potential as a
133 nurse-plant is known from Mediterrean grasslands (Boulant et al., 2008), but has not yet been
134 explored in forest systems. To understand the impact of ungulate browsing on the important
135 sapling stage of rowan populations and the potential benefits for rowan saplings of growing
136 under the protection of nurse-plants, we performed two long-term experiments. We first tested
137 A) how strongly ungulate browsing affects abundance and growth of rowan in a ten-year
138 ungulate exclosure experiment, with additional focus on the effects of browsing intensity.
139 Secondly, we B) investigated whether experimentally planting rowan saplings within juniper
140 could modify browsing damage, survival, and growth of rowan over a five-year period. As a
141 subset of question B, we also asked whether the potential nurse-effect was influenced by the
142 gradient in browsing intensity or modified by either juniper size or frost damage that could
143 influence its success as a nurse plant. Based on the attractiveness of rowan to large herbivores,
144 we expected rowan abundance and growth to be negatively related to ungulate browsing
145 intensity. Similarly, due to our field observations of possible nurse-plant effects, we expected
146 that rowan saplings growing within junipers would exhibit greater growth and survival
147 compared to controls, regardless of browsing intensity. Such investigations are likely to be
148 important to the study of facilitation in boreal forests and the potential to develop nurse-plants
149 as a conservation and management tool.

150 2. Materials and Methods

151 2.1 Study area

152 The study was conducted at the 11 km² Svanøy island, located in the outer part of the
153 Førdefjord, on the western coast of Norway (61°30'N, 5°05'E). Svanøy has an oceanic climate
154 with an annual mean temperature of 8.1 °C (as measured at Florø Airport, ca. 9 km away,
155 2006–2019) and annual precipitation of ca. 2300 mm (as measured at Tefre Sunnfjord, ca. 40
156 km away, 2001–2017; data from both stations of the most recent period available at
157 <https://seklima.met.no/observations>) and the island is located in the boreonemoral zone
158 (Moen, 1999). The island is mainly covered by old growth pine forest (*Pinus sylvestris*) and
159 has a rugged topography and elevations up to ca. 300 m. The understory layer is dominated
160 by Ericaceae dwarf-shrubs like bilberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idaea*)
161 and heather (*Calluna vulgaris*), various amounts of trees and bushes like juniper, birch
162 (*Betula* sp.), rowan, Swedish service tree (*Sorbus hybrida*), hazel (*Corylus avellana*), holly
163 (*Ilex aquifolium*) and aspen (*Populus tremula*; unpublished data S.J. Hegland). Coniferous
164 forest with understory dominated by dwarf-shrub and various trees, represents the most
165 common forest type in such boreal, or cool-temperate, ecosystems (Moen, 1999). The forest
166 on Svanøy is mainly grazed and browsed by large herbivores like red deer and free-ranging
167 domestic sheep (*Ovis aries*; documented on wildlife camera traps from 2011-2015;
168 unpublished data), both of which are considered mixed-feeders with similar diets and
169 therefore with comparable impacts on the systems in which they live (Bodmer, 1990;
170 Mysterud, 2000). The animal densities of wild and domestic ungulates in the Svanøy forest
171 are hard to assess precisely, but in the relative sense they can be evaluated as relatively high
172 for Norwegian forest. Based on a theoretical harvest rate of 20% for red deer, and the fact that
173 ca. 1.5 red deer/km² was harvested at Svanøy from 2000-2010 (pers. comm. J.T. Solheim), we
174 can estimate the mean density for the island to be ca. 7.5 deer/km². In the same period the

175 sheep population contained averagely ca. 150 adults (numbers from Kinn municipality, pers.
176 comm. J.A. Stavang) which gives a density of nearly 14 sheep/km². Sheep in Norway is
177 primarily free ranging in the summer season, but in some parts of the island sheep has also
178 been feeding during winter (pers.obs. S.J Hegland). Both previous to ca. year 2000 and the
179 last five years (the period of Exp. B, see below) the sheep number has been higher and is now
180 nearly 300 adults (pers. comm. J.A. Stavang). Based on personal observations and the
181 numbers available, we assume that the mean densities of the two ungulate species in the
182 forested parts of the Svanøy island are roughly equal for the period of Experiment A (see
183 2.2.), but may be higher for sheep in the period of Experiment B (see 2.3.).

184

185 *2.2. Experiment A: Browsing effects on rowan abundance and size*

186 We established ten study sites in winter 2000–2001, located in flat areas within old-growth
187 pine-bilberry forest, using a vegetation map (Skogen & Lunde, 1997). The ten sites were
188 spread across the island, minimum 300 m apart, at elevations between 20 and 140 metres
189 above sea level (see Hegland et al., 2005 for a map). Tree height and canopy openness
190 showed little variation between sites (Lilleeng et al., 2018). Each study site consisted of a pair
191 of 9 × 9 m plots. For each pair, one plot was within an ca. 10 × 10 m enclosure, ca. 2.5 m high
192 with wildlife fence and solid posts at ca. every 1 m, and one in an equal sized ungulate-access
193 control area located 10 to 50 m away from the enclosure.

194

195 To examine the effect of ungulate browsing on rowan abundance and size, we first counted
196 and mapped all tree saplings (immature individuals between 20 and 140 cm tall in 2001)
197 within each plot in 2001. This immature size class is in some herbivore studies referred to as
198 large seedlings (Bernes et al., 2018), but do not possess the characteristic cotyledons of
199 seedlings. The mapping allowed us to relocate all original saplings and map new individuals

200 in 2006 and 2011 (height range in 2011: 10 to 240 cm) to establish survival and recruitment in
201 addition to rowan density. In each study year, we also recorded rowan occurrence and height
202 (here measured to the closest 5 cm) of all saplings. We found that height alone was a good
203 predictor for aboveground plant size (dry mass) in a linear regression based on 71
204 independently sampled rowan plants ($R^2=0.97$). Plant height is therefore a good indicator of
205 plant size for the studied size class (see Appendix A for details).

206

207 To investigate the impact of variation in browsing intensities on rowan abundance, we
208 recorded the presence (yes/no) of pellets in hundred 1-m² quadrats randomly distributed
209 within a radius of 100 m around each of the ungulate-access control plots in 2001, 2006 and
210 2011. This frequency represents an index of relative ungulate density (Härkönen & Heikkilä,
211 1999) and is often directly related to browsing intensity (Hegland et al., 2005; Burkepile et al.,
212 2016). We used the mean pellet frequency (based on presence/absence) per site across years
213 which ranged from 0 to 25. Sampling in June made it difficult to distinguish between sheep
214 and red deer feces (i.e. less pellet-shaped than winter feces) and this study therefore focus on
215 the combined impact of these two species. From working with red deer and sheep, both in
216 research and as practioners for several decades, we have observed that except their size
217 differences they eat similar plants when they feed freely in ecosystems (pers. obs. S.J.
218 Hegland).

219

220 For all statistical analysis in this study we applied mixed effect modelling to account for the
221 spatial and temporal dependency among sampling units, using the R programming
222 environment (v4.0.2, R Development Core Team, 2020). To arrive at minimum adequate
223 models, all modelling was performed using backward stepwise selection to remove non-
224 significant factors, starting with interactions (Crawley, 2013). Residual diagnostics were

225 conducted using the ‘DHARMA’ package (Hartig, 2020), a package of diagnostic tools for
226 mixed models that takes a simulation-based approach to residual estimation. We used the
227 ‘car’ package (Fox & Weisberg, 2019) for calculating variance statistics, and the ‘emmeans’
228 package (Lenth, 2020) for estimating marginal means, standard errors and confidence
229 intervals for all models.

230

231 For analyses of the two responses in experiment A, abundance (number of trees in plots) and
232 plant height, the factors *treatment* (exclosure vs. ungulate-access), *year* (2001, 2006, 2011)
233 and their interaction were included as fixed effects, and site was used as random effect. We
234 analysed the experimental exclosure effect on rowan abundance from 2001 to 2011 with a
235 negative binomial generalised linear mixed model (GLMM) with the ‘glmmTMB’ package
236 (Brooks et al., 2017). Specifically, we used the negative binomial distribution with quadratic
237 parameterisation (nbinom2 family option) and the square root link function as this provided
238 the best fit to the data in terms of satisfactory residual plots. Growth data were unbalanced (18
239 recordings in ungulate-access controls vs 235 in exclosures) so these were not analysed
240 statistically but mean differences between 2006 and 2011 are presented in the results. Linear
241 regression was applied to investigate the relationship between browsing intensity (mean
242 frequency of pellets per site across the three sampling years) and the change in rowan
243 abundance from 2001 to 2011 in ungulate-access plots (n=10).

244

245 *2.3. Experiment B. Nurse-plant effect of juniper shrubs on rowan saplings*

246 The same ten study sites as in experiment A were used for the nurse-plant experiment (B). At
247 each site, four juniper bushes of approximately equal age and size (70 to 180 cm tall) were
248 selected ca. 25 m away from each side of the exclosure (i.e., to the north, east, south, and west
249 of the exclosure). We paired each juniper bush with open area in the ungulate-access control

250 area (see exp A) at 3 to 5 m. This resulted in 40 study pairs, four at each site, in which we
251 planted 80 rowan saplings (acquired from Aaberge plant nursery in Sogndal, western Norway)
252 on 10 September 2013. The plants were first randomly assigned to the sites, and then to the
253 two treatments: 1) saplings were planted within the juniper bush or 2) in paired field
254 vegetation without shrubs. The plants were marked with a tape, a stick and mapped by GPS-
255 coordinates to allow relocation.

256

257 We measured the height of rowan saplings of and their browsing damage at planting date
258 (Year 0), in June 2014 (Year 1), June 2015 (Year 2) and June 2018 (Year 5). Browsing
259 damage was recorded as a categorical variable (no browsing, light browsing, heavy browsing
260 or dead). Light browsing was defined as either browsing of one terminal shoot or one lateral
261 shoot (i.e., biomass removal < ca. 25%) and heavy browsing was all browsing above this
262 level.

263

264 For statistical analyses of experiment B, we used the same main approach as for experiment
265 A. The responses, browsing damage, including mortality, and plant height, were analysed by
266 using the factors *treatment* (protected or control), *year* (Years 0, 1, 2 & 5) and their
267 interaction as fixed effects, and pair nested within site as random effects. The effect of
268 treatment on plant height was modelled with a linear mixed effect model in the glmmTMB
269 package (gaussian family). The browsing damage represented an ordinal response and
270 attempts to fit logistic regression models with our random structure failed to converge or
271 violated the assumption of proportional odds. We therefore converted the four categories to a
272 binary response, combining the no and light browsing categories to represent low browsing
273 (0), and combining the heavy and dead browsing categories to represent high herbivore

274 damage (1). We then analysed this response with a binomial GLMM (in glmmTMB) with a
275 logit link.

276

277 Using the pellet frequency (see experiment A), we also investigated whether there was a
278 modifying effect of browsing intensity on the nurse-plant effect. We repeated the analysis for
279 plant height and browsing damage above, including the pellet frequency as a fixed effect, as
280 well as *year* and the interaction. In addition, we took advantage of a natural experiment at the
281 study sites when 24 of the 40 juniper nurse plants suffered severe frost damage during the
282 winter of 2015 (Year 2) causing full, or partial browning and often increased mortality in
283 junipers. We tested the impact of this frost damage on the nurse-plant effect by repeating the
284 analyses for plant height and browsing damage on protected rowan plants but with the factor
285 *frost damage* (yes/no) as fixed effect and site as random effect. To complete the analysis of
286 how height and other characteristics of juniper could influence its “nursing” abilities we also
287 included an analysis of the effect of juniper size, measured as the widest canopy diameter as
288 this could impact ungulate access to rowan plants, using the same statistical approach as for
289 the frost damaged plants.

290

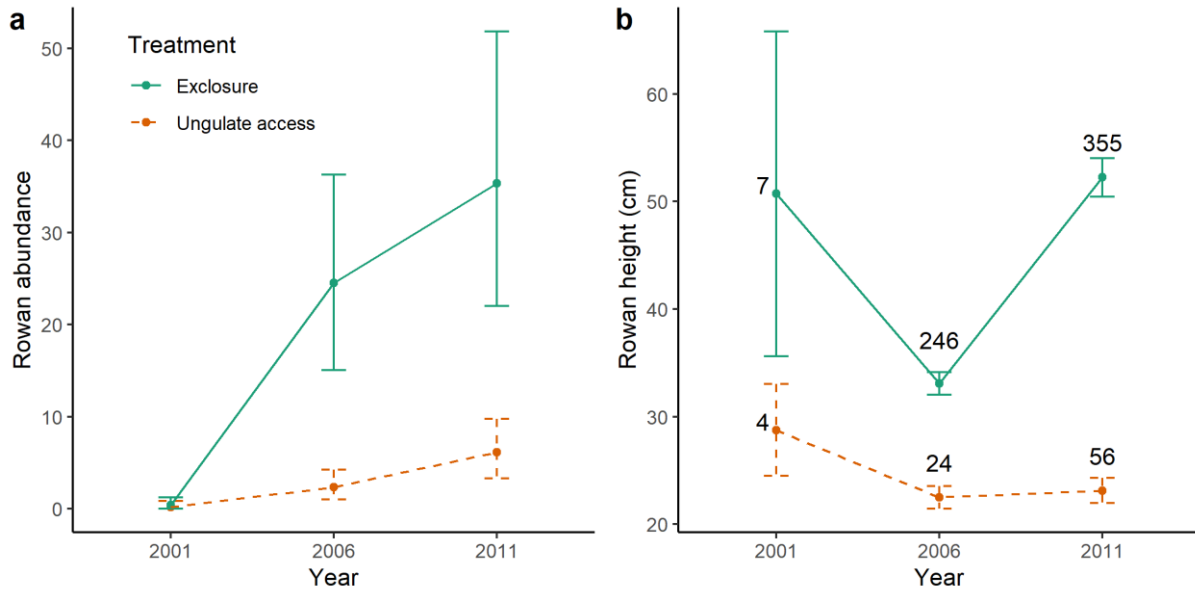
291 3. Results

292 3.1. A: Browsing effects on rowan abundance and height

293 Excluding ungulates had a significant positive effect on rowan abundance (*year*treatment*
294 interaction type III Wald $\chi^2 = 38.06$, $p < 0.001$; Fig. 1a). At the start of the enclosure-
295 experiment, in 2001, we found in total 7 individuals in enclosure plots within the size class
296 20–140 cm vs. 5 in ungulate-access plots. By 2011 these numbers had increased to 357 (0.44

297 rowan/m²) vs. 56 (0.07 rowan/m²) saplings, i.e., more than six times more rowan in exclosures
298 than in ungulate-access plots.

299



300

301 **Figure 1.** Rowan abundance (a; mean number of individuals in 9 x 9 m plots) and b) mean
302 rowan height in exclosures and ungulate-access plots from 2001 to 2011 in large herbivore
303 exclosures (n= 10) and ungulate-access plots (n=10) in old-growth forest at Svanøy Island,
304 western Norway. Diagram a) depicts predicted marginal mean abundances estimated from a
305 negative binomial GLMM with square root link function for the exclosure and ungulate-
306 access plots and error bars as 95% confidence intervals; b) are calculated means, with
307 sampling numbers in black and error bars are 1 SE.

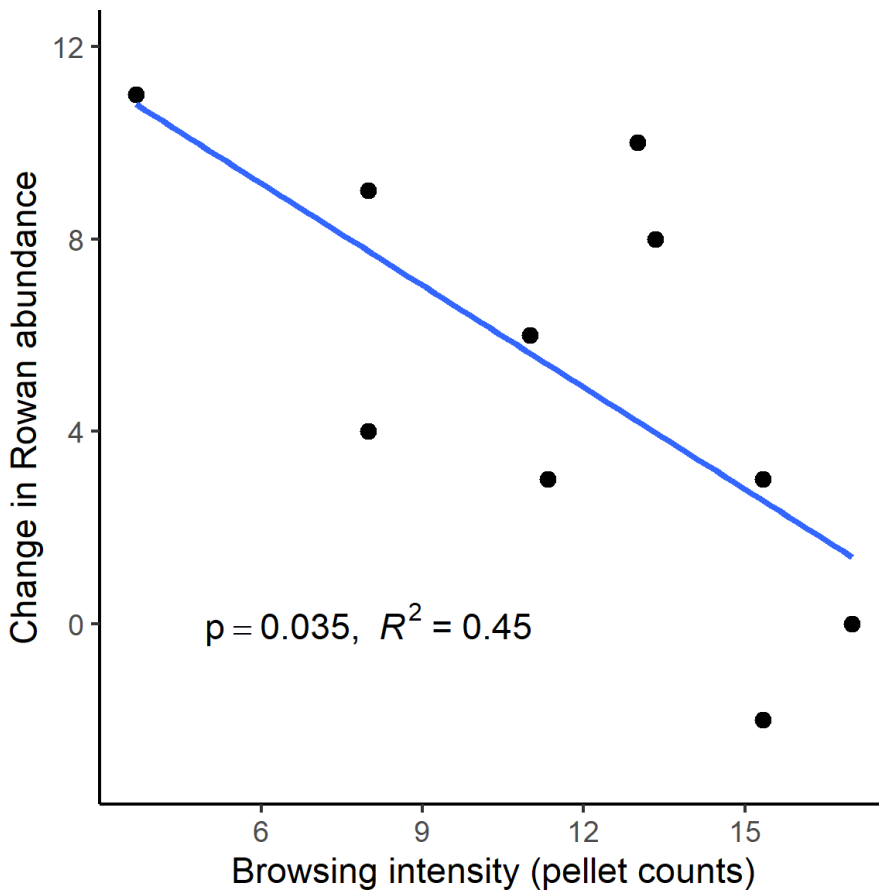
308

309 The unbalanced individual-based growth data could not be analysed statistically (see Material
310 and methods), but the exclosure plants that had survived were by 2011 almost twice as tall as
311 the rowans in ungulate-access plots (Fig. 1b; mean height of 52.2 cm \pm 1.8 SE vs mean height
312 of 23.1 cm \pm 4.3 SE) and had reached a maximum height of 230 cm in the exclosures vs. 60
313 cm in the ungulate access plots. The smaller mean height of the exclosure population in 2006
314 than 2001 (Fig. 1b) is a direct consequence of the large increase in juvenile rowans (Fig. 1a)

315

316 Browsing intensity, or relative ungulate density, affected the abundance of rowan saplings
317 negatively as the mean pellet frequency (data from 2001, 2006 and 2011) showed a significant
318 negative relationship with the change in rowan abundance from 2001 to 2011 (Fig 2, slope = -
319 0.71 ± 0.3 SE $t = -2.5$, $p = 0.035$).

320



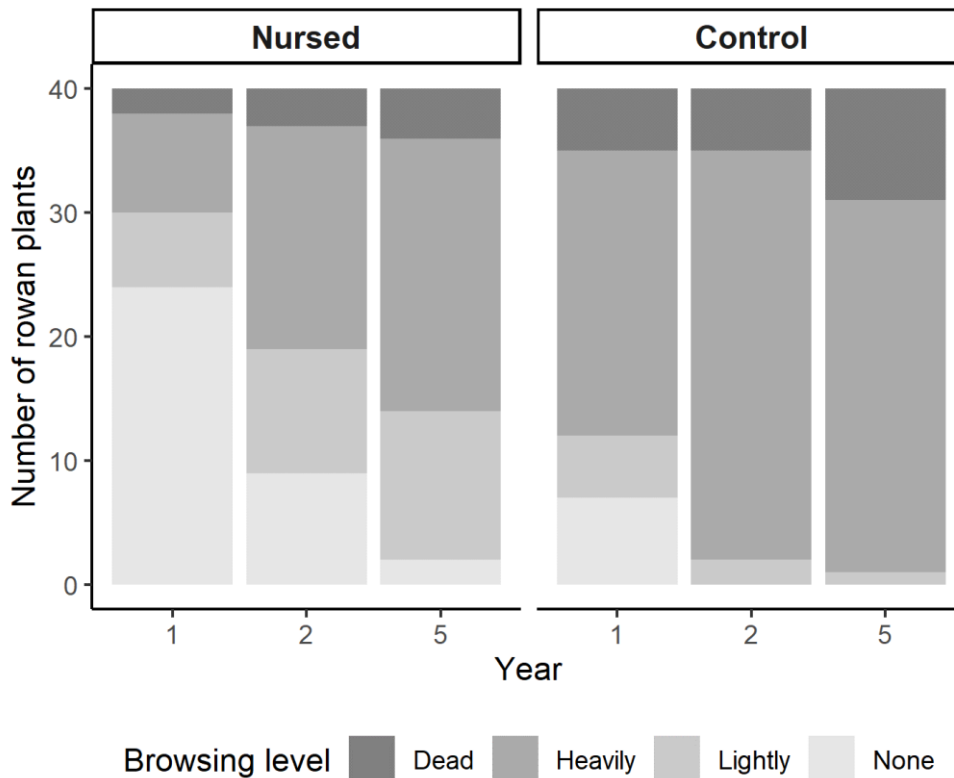
321

322 **Figure 2.** Change in rowan abundance (mean number of individuals) as a function of
323 browsing intensity in old-growth forest at Svanøy Island, western Norway. Abundance is
324 calculated as difference between 2011 and 2001 recordings, and browsing intensity is
325 measured as mean frequency of pellets (presence/absence in 100 quadrats) around ungulate
326 access plots (n=10) from 2001, 2006 and 2011. The blue line represents the linear regression
327 line.

328

329 3.2. B: Nurse-plant effect of juniper shrubs on rowan saplings

330 Seventy percent of unprotected control plants experienced heavy browsing damage (categories
331 heavily browsed or dead) after the first winter, compared to only 25% of the protected saplings
332 (Fig. 3). This difference between treatments was reduced over time as more protected plants
333 were browsed, but after five years there was still 50% more heavy browsing damage in control
334 (98%) than in protected plants (65%, Fig. 3) and twice as many dead rowan saplings when
335 unprotected. The mortality of saplings was also more than twice as high in control (23%) vs.
336 protected (10% dead) plants after five years (Fig. 3).



337

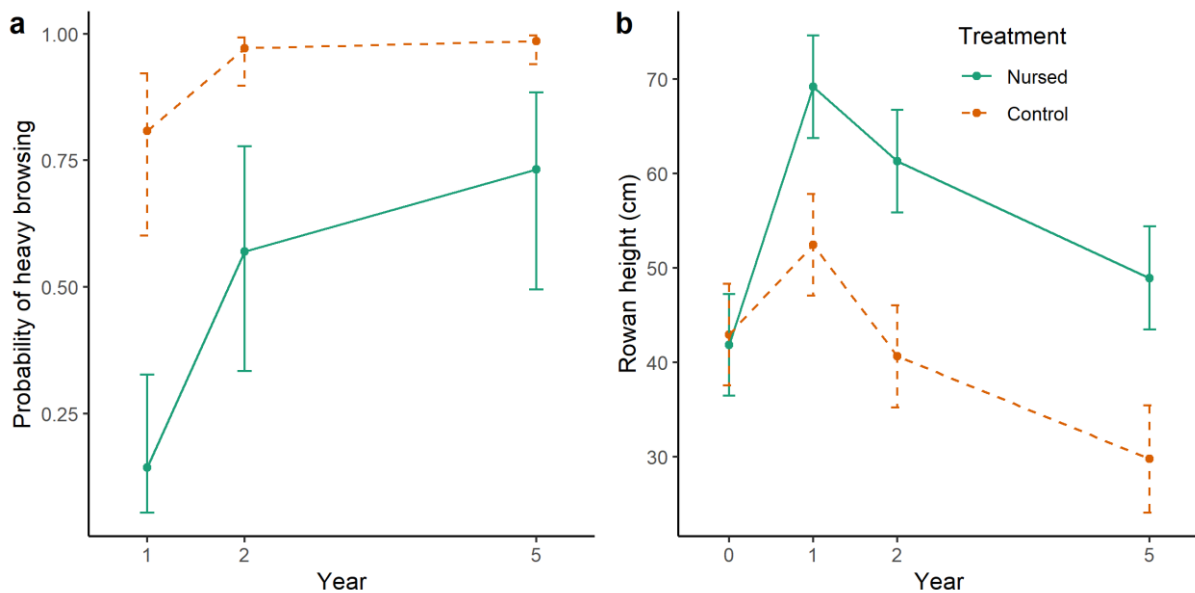
338 **Figure 3.** The browsing pressure (no browsing, lightly or heavily browsed, and dead from
339 browsing) protected (n=40) and control (n=40) saplings of rowan (*Sorbus aucuparia*) from year
340 1 (2014) to year 5 (2018) at ten sites in old-growth forest at Svanøy Island, western Norway.

341

342 Testing these patterns with the binomial GLMM revealed that there was a significant effect of
 343 treatment (Fig. 4a; type II Wald $\chi^2= 36.5$, $p < 0.001$), with the control plants more likely to be
 344 browsed heavily than protected plants. There was also a significant effect of year (Fig. 4a; type
 345 II Wald $\chi^2= 25.4$, $p < 0.001$), but no significant interaction between treatment and year
 346 indicating that the nurse-plant effect was not dependent on year. The mean probability of heavy
 347 browsing was more than 0.75 after one year in unprotected control plants, and already
 348 approaching 1 in subsequent years (Fig. 4a). Conversely, this probability was still below 0.75
 349 after five years in protected plants.

350

351 The growth was nearly 50% higher in protected (+16%) vs. unprotected saplings (-30%) over
 352 the five years (Fig. 4b). The linear mixed model for plant height had a significant *treatment x*
 353 *year* interaction (type III Wald $\chi^2= 36.2$, $p < 0.001$), which was largely due to a difference in
 354 growth in the first year (Fig. 4b), indicating that protected rowan stayed consistently taller than
 355 unprotected control plants throughout the study period.



356

357 **Figure 4.** Changes in (a) probability of heavy browsing damage and in (b) mean plant height
 358 of rowan saplings protected by juniper (n=40) and in open controls (n = 40) across the
 359 sampling years (Year 0 = 2013, 5=2018) in an old-growth forest at Svanøy Island, western

360 Norway. The diagrams show the predicted marginal mean from mixed effects models. Error
361 bars are 95% confidence intervals.

362

363 We found no significant effect of the index of browsing intensity (i.e., pellet frequency) on
364 either the probability of heavy browsing damage (type II Wald $\chi^2 = 2.2$, $p = 0.142$) or the height
365 of rowan saplings (type II Wald $\chi^2 = 0.6$, $p = 0.439$). There was no significant effect of juniper
366 size on the responses of protected rowan plants in terms of browsing damage (juniper height:
367 type II Wald $\chi^2 = 0.5$, $p = 0.477$; juniper canopy diameter: type II Wald $\chi^2 = 0.1$, $p = 0.778$) or
368 rowan height (juniper height: type II Wald $\chi^2 = 0.0$, $p = 0.844$; juniper canopy diameter: type II
369 Wald $\chi^2 = 0.3$, $p = 0.576$). Rowan planted within juniper bushes that were frost damaged tended
370 to be more heavily browsed after five years than rowan planted in undamaged juniper bushes
371 (30% more), but the difference was not statistically significant (type II Wald $\chi^2 = 2.3$, $p =$
372 0.120 ; significant year effect: type II Wald $\chi^2 = 12.9$, $p = 0.002$). The frost damage effect on
373 growth also tended to increase browsing damage, but was not statistically significant (type II
374 Wald $\chi^2 = 1.74$, $p = 0.190$; Year: type II Wald $\chi^2 = 24.5$, $p < 0.001$).

375 4. Discussion

376 In this study, we demonstrated that rowan abundance and growth were strongly impacted by
377 the combination of wild and domestic ungulate browsing in a boreal, cool-temperate, forest
378 ecosystem. We found, by means of experimental plantings, that rowan saplings could escape
379 ungulate browsing, and improve their survival and growth in the long term, by growing within
380 nurse-plants of juniper.

381

382 The six-fold higher increase in rowan abundance in exclosures over ungulate-access plots
383 (Exp. A), as well as the large abundance changes along the browsing intensity gradient,
384 strongly reflects the impact of ungulate feeding on rowan recruitment and performance. The

385 clear negative effect of browsing on the abundance of rowan saplings is unsurprising given
386 that decline in woody species abundance, in particular the immature sapling stage, is a
387 hallmark of large herbivore impact (Hegland & Rydgren, 2016). However, the large increase
388 in abundance over time when excluding deer and sheep to 0.44 rowans/m² opposed to only
389 0.07 rowans/m² in ungulate-access plots is perhaps more remarkable than shown in most
390 previous studies. Although there are variation in plant species responses to excluding
391 ungulates (Fortuny et al., 2020), other studies comparable in design, study period and
392 ungulate species have typically found that exclosures exhibit around double the increase in
393 rowan abundance over time compared to controls (Speed et al., 2013; Nopp-Mayr et al.,
394 2020). The effect of excluding deer and sheep in our study is more equivalent to that found
395 when excluding the most typical browser of northern ecosystems, the moose (*Alces alces*),
396 from clear-cuts (Kolstad et al., 2018), a habitat that typically offers better conditions for
397 germination of rowan than shaded old-growth forest. Clearly the large change in rowan
398 abundance along the herbivory gradient shows that the density of ungulates plays a decisive
399 role for the population dynamics of rowan, and possibly other deciduous tree species also in
400 old-growth forest. The variation in animal densities among the sites at Svanøy may have
401 facilitated such findings, which do point to important management related applications. The
402 consistency between the result from the exclosure- and the gradient-based approach also
403 justifies the characterisation of rowan as a herbivory “loser” and thus a species that may be
404 used to indicate browsing pressure in boreal forest (Hegland & Rydgren, 2016).

405

406 Our finding that the height of rowan in exclosures was double that of ungulate-access plots,
407 coupled with the lack of rowan above 60 cm in browsed areas (compared to max 230 cm in
408 exclosures) after ten years of excluding ungulates (Exp. A), underlines the structuring role of
409 these herbivores in such forest systems. Moe et al. (2014) stated that among the main

410 herbivore guilds (i.e. grazers, mixed feeders and browsers), the mixed feeders may have the
411 largest negative effect on tree seedlings, whereas browsers may in reality enhance seedling
412 recruitment by removing larger size classes of woody competitors. It appears that at Svanøy
413 the red deer and sheep, classified as mixed-feeders, act as functional browsers when they feed
414 in forest. Such characterisation is based on the contrasting effect of the large herbivore effects
415 we find for different size classes of rowan, i.e. the positive or neutral effect on <20 cm rowan
416 (“seedlings”/young saplings) and the clearly negative, “moose-like”, effect on 20-240 cm
417 rowan (saplings) at Svanøy (Hegland & Rydgren, 2016; current study). Several authors have
418 pointed to a “browse trap” (Staver & Bond, 2014) of about 50 cm for tree saplings to survive
419 browsing and grow into adult stages in forests (D. Kuijper et al., 2010; Speed et al., 2013),
420 and this threshold appears to be applicable also in our system. Moreover, a meta-analysis by
421 Bernes et al. (2018) showed that small seedlings (< 30 cm) overall are not negatively
422 impacted by high herbivore densities in boreal and temperate forest whereas saplings most
423 often are. That few deciduous saplings of species like rowan survive in browsed landscapes
424 may likely alter successional trajectories and influence forest species composition for several
425 decades (Tremblay et al., 2007; Hidding et al., 2013; Nuttle et al., 2014). Long-term datasets
426 on oak (*Quercus robur*) regeneration from Sweden showed that, in addition to the trend
427 towards denser and darker forests over the last decades, increased wild ungulate abundance is
428 the second most important determinant of tree recruitment (Pettersson et al., 2019). In the
429 relatively open canopy of the old-growth pine-bilberry forest at Svanøy, there was an increase
430 in abundance of rowan saplings (< 60 cm) even in unfenced sites that point to a recruitment
431 potential and, to some extent, tolerance of rowan to herbivore browsing. We showed that
432 browsing intensity, and hence the combined density of deer and sheep, may play a crucial role
433 for how this recruitment potential is enabled.

434

435 Juniper clearly had a nurse-plant effect on rowan by reducing browsing pressure and
436 increasing survival and growth of planted saplings, both in the short- and long-term (Exp. B).
437 These results confirm our hypothesis of an escape for rowan in nurse plants from browsing by
438 large ungulates, also in boreal forest. The magnitude of reduced browsing on saplings, i.e., ca.
439 50% difference between treatments after 5 years, was comparable to the few other
440 experimental nurse-plant studies performed in late successional forest. Jensen et al. (2012)
441 found that nurse shrubs reduced browsing frequency of oak seedlings in a Swedish deciduous
442 forest by up to 30% compared to control plants. Similarly, Bannister (2020) found ca. 50%
443 reduction in browsing of a target conifer seedling when shrubs were retained in a Chilean bog
444 forest. However, our study appears as one of the first to target saplings, or larger juveniles, a
445 stage class for which survival is probably the most decisive for the recovery of tree
446 populations in browser dominated forest systems (D. Kuijper et al., 2010; Speed et al., 2013;
447 Staver & Bond, 2014).

448

449 Our subsequent finding that reduced browsing of protected saplings positively affected
450 survival and growth also point towards a long-term facilitation effect of the interaction with
451 the nurse plant juniper (Exp. B). For example, there were twice as many dead unprotected
452 rowan plants after five years than among the protected plants. Also, the unprotected plants
453 that survived were more frequently heavily browsed, and therefore experienced nearly half the
454 height compared to the protected rowan. It should be mentioned that also protected plants
455 showed decreased mean height during the five-year study. We ascribe this size reduction to
456 the fact that some individuals are browsed also when protected, and that the herbivore
457 protection from juniper is only partial (Fig. 3). Outcomes on plant survival and size (or
458 growth) are highly variable across other nurse-plant studies depending on factors related to
459 traits of nurse-plants, life stages of protected plants as well as the environmental conditions

460 (Brooker et al., 2006; Brooker et al., 2008). We showed consistent nurse-plant effects across
461 the response variables, i.e., from reduced browsing to increased survival and growth, and the
462 beneficial effects lasted over time. In our system the facilitative effect was not even dependent
463 (at least not statistically) on the characteristics of the nurse-plant (size variables and vitality
464 reduction by frost damage) or the environmental gradient in terms of browsing intensity. In
465 sum, this indicated that juniper's facilitative effects were strong, and outweighed the
466 potentially competing influence for light, water, and nutrients, resulting in a net positive
467 influence on the fitness of the protected rowan plants in the browsed landscape of Svanøy.
468

469 Net positive effects of the nurse-plant interactions may be very important in old growth
470 forests like our study system. The forest understorey, as well as the overstorey canopy, often
471 acts as a competitive filter reducing the emergence, survival, density and growth of tree
472 juveniles (Landuyt et al., 2019). Landuyt et al. (2019) suggested that when herbivory plays an
473 important ecological role in an ecosystem, the understorey may have a net positive effect on
474 plants in need of protection. Also, they advocated that browsing itself may indirectly facilitate
475 tree recruitment by gap-creation in dense understoreys that otherwise would outcompete small
476 trees for light and nutrients, indicating a rather complex interplay of factors for the
477 recruitment of trees. Previous research at Svanøy indeed showed that increasing browsing
478 intensity up to relatively high levels benefitted both rowan juveniles (<20 cm) and the
479 diversity and abundance of all juvenile tree species (Hegland et al., 2013; Hegland &
480 Rydgren, 2016). Meta-analyses of large herbivore impact in temperate and boreal forest have
481 confirmed that saplings are largely negatively impacted by browsing, whereas small juveniles
482 are often not (Bernes et al., 2018). Juvenile trees may thus often be protected when growing
483 within a field or shrub layer vegetation, but then browsed intensively when they grow out of
484 this protecting ground canopy, thus reach the browse-trap size, and therefore stop gaining

485 biomass (Miller et al., 1982; Palmer & Truscott, 2003; Brooker et al., 2006; Peláez et al.,
486 2019). Consequently, many nurse-plant relationships are transient, and palatable plants
487 susceptible to large herbivore damage may require several facilitative “partners” or
488 “neighbours” throughout their life cycle. In our system, juniper may provide an effective
489 partner until rowan has passed the browse trap phase, but further research is required to
490 investigate the quantitative impact of juniper facilitation after this phase, including potential
491 competitive and reciprocal effects.

492 5. Conclusion

493 The implications of our findings, over 10 (Exp. A) + 5 (Exp. B) years of field experiments,
494 are multiple. Under increasing ungulate densities and intensified large herbivore impact in
495 many ecosystems of the Northern hemisphere, enclosure experiments like ours (Exp. A) have
496 improved our understanding of the herbivory effect on forest vegetation. We showed that a
497 functionally important tree species was heavily affected by browsing in terms of abundance
498 (1/6 of saplings) and growth (1/2 of size) and that the relative density of ungulates is also a
499 strong determinant for change in rowan abundance. Furthermore, we presented evidence
500 (Exp. B) that the strong herbivore-induced reductions in plant abundance and size on the
501 functionally important tree species rowan may be counteracted by a positive plant-plant
502 interaction that reduced browsing damage (50% less) and mortality, (twice as high in
503 unprotected plants), and increased growth (>50% taller saplings) after five years in the
504 protected rowan plants. In sum, these positive nurse-plant effects may represent a persistent
505 escape mechanism for rowan saplings in browsed landscapes that facilitates recovery of
506 rowan, and other tree, populations. Also, it may point to some long-term buffering feedback
507 mechanisms in these systems. For example, browsing may reduce deciduous tree abundance
508 providing the space for increased amounts of the conifers like juniper. This shrub may then, as
509 our results show, facilitate the recruitment of the herbivore-preferred and deciduous tree,

510 rowan. Maintaining forest ecosystems consisting of multi-layered and multi-species
511 understoreys is thus vital to preserve plant recruitment processes and mitigate succession
512 patterns. Nurse-plant effects may be one of several buffering mechanisms of the understoreys
513 in mixed forests that could be actively stimulated in forestry and conservation management.
514 Such mechanisms will be increasingly important in rewilded landscapes that are also heavily
515 impacted by human activities.

516 CRediT authorship contribution statement

517 **Stein Joar Hegland**: Funding acquisition, Conceptualisation, Methodology, Investigation,
518 Formal analysis, Writing – Original Draft; Writing – Review & Editing; **Knut Rydgren**:
519 Formal analysis, Validation, Writing – Review & Editing; **Marte Lilleeng**: Investigation,
520 Validation, Writing – Review & Editing; **Stein Moe**: Validation, Writing – Review &
521 Editing; **Mark Gillespie**: Formal Analysis, Visualisation, Writing – Review & Editing
522

523 Declaration of competing interest

524 The authors declare that there is no conflict of interest.

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529 References

530 Bannister, J. R., Travieso, G., Galindo, N., Acevedo, M., Puettmann, K., & Salas-Eljatib, C.
531 (2020). Shrub influences on seedling performance when restoring the slow-growing
532 conifer *Pilgerodendron uviferum* in southern bog forests. *Restoration Ecology*, 28,
533 396-407. <https://doi.org/10.1111/rec.13090>

- 534 Bee, J. N., Tanentzap, A. J., Lee, W. G., Lavers, R. B., Mark, A. F., Mills, J. A., & Coomes,
535 D. A. (2009). The benefits of being in a bad neighbourhood: plant community
536 composition influences red deer foraging decisions. *Oikos*, *118*, 18-24.
537 <https://doi.org/10.1111/j.1600-0706.2008.16756.x>
- 538 Bernes, C., Macura, B., Jonsson, B. G., Junninen, K., Müller, J., Sandström, J., Lõhmus, A.,
539 & Macdonald, E. (2018). Manipulating ungulate herbivory in temperate and boreal
540 forests: effects on vegetation and invertebrates. A systematic review. *Environmental*
541 *Evidence*, *7*, 13. <https://doi.org/10.1186/s13750-018-0125-3>
- 542 Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in*
543 *Ecology & Evolution*, *9*, 191-193. ISI:A1994NF67300014
- 544 Bodmer, R. E. (1990). Ungulate frugivores and the browser-grazer continuum. *Oikos*, *57*,
545 319-325.
- 546 Boulant, N., Navas, M.-L., Corcket, E., & Lepart, J. (2008). Habitat amelioration and
547 associational defence as main facilitative mechanisms in Mediterranean grasslands
548 grazed by domestic livestock. *Ecoscience*, *15*, 407-415. <https://doi.org/10.2980/15-3-3126>
- 549
- 550 Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G.,
551 Liancourt, P., Tielborger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L.,
552 Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.
553 L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., & Michalet, R. (2008).
554 Facilitation in plant communities: the past, the present, and the future. *Journal of*
555 *Ecology*, *96*, 18-34. <https://doi.org/doi:10.1111/j.1365-2745.2007.01295.x>
- 556 Brooker, R. W., Scott, D., Palmer, S. C. F., & Swaine, E. (2006). Transient facilitative effects
557 of heather on Scots pine along a grazing disturbance gradient in Scottish moorland.
558 *Journal of Ecology*, *94*, 637-645. <https://doi.org/10.1111/j.1365-2745.2006.01129x>
- 559 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A.,
560 Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and
561 flexibility among packages for zero-inflated generalized linear mixed modeling. *R*
562 *Journal*, *9*, 378-400. <https://doi.org/10.32614/rj-2017-066>
- 563 Bråthen, K. A., & Lortie, C. (2016). A portfolio effect of shrub canopy height on species
564 richness in both stressful and competitive environments. *Functional Ecology*, *30*, 60-
565 69. <https://doi.org/10.1111/1365-2435.12458>
- 566 Burkepile, D. E., Thompson, D. I., Fynn, R. W. S., Koerner, S. E., Eby, S., Govender, N.,
567 Hagenah, N., Lemoine, N. P., Matchett, K. J., Wilcox, K. R., Collins, S. L., Kirkman,
568 K. P., Knapp, A. K., & Smith, M. D. (2016). Fire frequency drives habitat selection by
569 a diverse herbivore guild impacting top-down control of plant communities in an
570 African savanna. *Oikos*, *125*, 1636-1646.
571 <https://doi.org/https://doi.org/10.1111/oik.02987>
- 572 Callaway, R. M. (1995). Positive interactions among plants. *Botanical Review*, *61*, 306-349.
- 573 Churski, M., Bubnicki, J. W., Jędrzejewska, B., Kuijper, D. P. J., & Cromsigt, J. P. G. M.
574 (2017). Brown world forests: increased ungulate browsing keeps temperate trees in
575 recruitment bottlenecks in resource hotspots. *New Phytologist*, *214*, 158-168.
576 <https://doi.org/10.1111/nph.14345>
- 577 Crawley, M. (2013). *The R book* (2nd ed.). John Wiley & Sons.
- 578 Danell, K., Bergstrom, R., Edenius, L., & Ericsson, G. (2003). Ungulates as drivers of tree
579 population dynamics at module and genet levels. *Forest Ecology and Management*,
580 *181*, 67-76.
- 581 Edenius, L., & Ericsson, G. (2015). Effects of ungulate browsing on recruitment of aspen and
582 rowan: a demographic approach. *Scandinavian Journal of Forest Research*, *30*, 283-
583 288. <https://doi.org/10.1080/02827581.2014.999823>

- 584 Filazzola, A., & Lortie, C. J. (2014). A systematic review and conceptual framework for the
585 mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, 23, 1335-
586 1345. <https://doi.org/10.1111/geb.12202>
- 587 Fortuny, X., Carcaillet, C., & Chauchard, S. (2020). Selective and taxon-dependent effects of
588 semi-feral cattle grazing on tree regeneration in an old-growth Mediterranean
589 mountain forest. *Forest Ecosystems*, 7, 11. <https://doi.org/10.1186/s40663-020-00222-7>
- 590
- 591 Fox, J., & Weisberg, S. (2019). *An {R} Companion to Applied Regression* (Vol. 3). Sage.
592 <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- 593 Gomez-Aparicio, L. (2009). The role of plant interactions in the restoration of degraded
594 ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, 97,
595 1202-1214. <https://doi.org/10.1111/j.1365-2745.2009.01573.x>
- 596 Gomez-Aparicio, L., Zamora, R., Gomez, J. M., Hodar, J. A., Castro, J., & Baraza, E. (2004).
597 Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs
598 as nurse plants. *Ecological Applications*, 14, 1128-1138. <https://doi.org/10.1890/03-5084>
- 599
- 600 Harmer, R., Kiewitt, A., Morgan, G., & Gill, R. (2010). Does the development of bramble
601 (*Rubus fruticosus* L. agg.) facilitate the growth and establishment of tree seedlings in
602 woodlands by reducing deer browsing damage? *Forestry: An International Journal of*
603 *Forest Research*, 83, 93-102. <https://doi.org/10.1093/forestry/cpp032>
- 604 Hartig, F. (2020). *DHARMA: Residual diagnostics for hierarchical (multi-level / mixed)*
605 *regression models*. <https://CRAN.R-project.org/package=DHARMA>
- 606 Hegland, S. J., Lilleeng, M. S., & Moe, S. R. (2013). Old-growth forest floor richness
607 increases with red deer herbivory intensity. *Forest Ecology and Management*, 310,
608 267-274. <https://doi.org/http://dx.doi.org/10.1016/j.foreco.2013.08.031>
- 609 Hegland, S. J., & Rydgren, K. (2016). Eaten but not always beaten: winners and losers along a
610 red deer herbivory gradient in boreal forest. *Journal of Vegetation Science*, 27, 111-
611 122. <https://doi.org/10.1111/jvs.12339>
- 612 Hegland, S. J., Rydgren, K., & Seldal, T. (2005). The response of *Vaccinium myrtillus* to
613 variations in grazing intensity in a Scandinavian pine forest on the island of Svanøy.
614 *Canadian Journal of Botany*, 83, 1638-1644.
615 <https://doi.org/https://doi.org/10.1139/b05-132>
- 616 Hidding, B., Tremblay, J.-P., & Côté, S. D. (2013). A large herbivore triggers alternative
617 successional trajectories in the boreal forest. *Ecology*, 94, 2852-2860.
618 <https://doi.org/10.1890/12-2015.1>
- 619 Hjeljord, O., Histøl, T., & Wam, H. (2014). Forest pasturing of livestock in Norway: effects
620 on spruce regeneration. *Journal of Forestry Research*, 25, 941-945.
621 <https://doi.org/10.1007/s11676-014-0487-5>
- 622 Holmgren, M., & Scheffer, M. (2010). Strong facilitation in mild environments: the stress
623 gradient hypothesis revisited. *Journal of Ecology*, 98, 1269-1275.
624 <https://doi.org/10.1111/j.1365-2745.2010.01709.x>
- 625 Härkönen, S., & Heikkilä, R. (1999). Use of pellet group counts in determining density and
626 habitat use of moose *Alces alces* in Finland. *Wildlife Biology*, 5, 233-239.
- 627 Jensen, A. M., Götmark, F., & Löf, M. (2012). Shrubs protect oak seedlings against ungulate
628 browsing in temperate broadleaved forests of conservation interest: A field
629 experiment. *Forest Ecology and Management*, 266, 187-193.
630 <https://doi.org/https://doi.org/10.1016/j.foreco.2011.11.022>
- 631 Kolstad, A. L., Austrheim, G., Solberg, E. J., De Vriendt, L., & Speed, J. D. M. (2018).
632 Pervasive moose browsing in boreal forests alters successional trajectories by severely

- 633 suppressing keystone species. *Ecosphere*, 9, e02458.
634 <https://doi.org/10.1002/ecs2.2458>
- 635 Kuijper, Cromsigt, J. P. G. M., Jedrzejewska, B., Miscicki, S., Churski, M., Jedrzejewski, W.,
636 & Kweczlich, I. (2010). Bottom-up versus top-down control of tree regeneration in the
637 Bialowieza Primeval Forest, Poland. *Journal of Ecology*, 98, 888-899.
638 <https://doi.org/10.1111/j.1365-2745.2010.01656.x>
- 639 Kuijper, D., Jedrzejewska, B., Brzeziecki, B., Churski, M., Jedrzejewski, W., & Żybura, H.
640 (2010). Fluctuating ungulate density shapes tree recruitment in natural stands of the
641 Białowieża Primeval Forest, Poland. *Journal of Vegetation Science*, 21, 1082-1098.
642 <https://doi.org/10.1111/j.1654-1103.2010.01217.x>
- 643 Landuyt, D., De Lombaerde, E., Perring, M. P., Hertzog, L. R., Ampoorter, E., Maes, S. L.,
644 De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B. K., Wang, B., Wasof,
645 S., & Verheyen, K. (2019). The functional role of temperate forest understorey
646 vegetation in a changing world. *Global Change Biology*, 25, 3625-3641.
647 <https://doi.org/10.1111/gcb.14756>
- 648 Laskurain, N. A., Aldezabal, A., Olano, J. M., Loidi, J., & Escudero, A. (2013).
649 Intensification of domestic ungulate grazing delays secondary forest succession:
650 evidence from exclosure plots. *Journal of Vegetation Science*, 24, 320-331.
651 <https://doi.org/10.1111/j.1654-1103.2012.01469.x>
- 652 Lenth, R. (2020). *emmeans: Estimated Marginal Means, aka Least-Squares Means*.
653 <https://CRAN.R-project.org/package=emmeans>
- 654 Lilleeng, M. S., Hegland, S. J., Rydgren, K., & Moe, S. R. (2016). Red deer mediate spatial
655 and temporal plant heterogeneity in boreal forests [journal article]. *Ecological*
656 *Research*, 31, 777-784. <https://doi.org/10.1007/s11284-016-1391-6>
- 657 Lilleeng, M. S., Rydgren, K., Halvorsen, R., Moe, S. R., & Hegland, S. J. (2018). Red deer
658 structure the ground-dwelling beetle community in boreal forest. *Biodiversity and*
659 *Conservation*, 27, 2507–2525. <https://doi.org/10.1007/s10531-018-1550-x>
- 660 Löf, M., Ammer, C., Coll, L., Drössler, L., Huth, F., Madsen, P., & Wagner, S. (2018).
661 Regeneration patterns in mixed-species stands. In A. Bravo-Oviedo, H. Pretzsch, & M.
662 del Río (Eds.), *Dynamics, Silviculture and Management of Mixed Forests* (pp. 103-
663 130). Springer International Publishing. https://doi.org/10.1007/978-3-319-91953-9_4
- 664 Löf, M., Bolte, A., Jacobs, D. F., & Jensen, A. M. (2014). Nurse trees as a forest restoration
665 tool for mixed plantations: effects on competing vegetation and performance in target
666 tree species. *Restoration Ecology*, 22, 758-765. <https://doi.org/10.1111/rec.12136>
- 667 Mayer, C., Michez, D., Chyzy, A., Bredat, E., & Jacquemart, A. L. (2012). The abundance
668 and pollen foraging behaviour of bumble bees in relation to population size of
669 whortleberry (*Vaccinium uliginosum*). *PLoS ONE*, 7, e50353.
670 doi:50310.51371/journal.pone.0050353, Article e50353.
671 <https://doi.org/10.1371/journal.pone.0050353>
- 672 McInnes, P. F., Naiman, R. J., Pastor, J., & Cohen, Y. (1992). Effects of moose browsing on
673 vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*, 73,
674 2059-2075.
- 675 McIntire, E. J. B., & Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity.
676 *New Phytologist*, 201, 403-416. <https://doi.org/10.1111/nph.12478>
- 677 Miller, G. R., Kinnaird, J. W., & Cummins, R. P. (1982). Liability of saplings to browsing on
678 a red deer range in the Scottish highlands. *Journal of Applied Ecology*, 19, 941-951.
679 <https://doi.org/10.2307/2403295>
- 680 Milne-Rostkowska, F., Holeksa, J., Bogdziewicz, M., Piechnik, Ł., Seget, B., Kurek, P.,
681 Buda, J., & Żywiec, M. (2020). Where can palatable young trees escape herbivore

682 pressure in a protected forest? *Forest Ecology and Management*, 472, 118221.
683 <https://doi.org/https://doi.org/10.1016/j.foreco.2020.118221>

684 Moe, S. R., Rutina, L. P., Hytteborn, H., & du Toit, J. T. (2014). Impala as controllers of
685 elephant-driven change within a savanna ecosystem. In C. Skarpe, J. T. du Toit, & S.
686 R. Moe (Eds.), *Elephants and savanna woodland ecosystems: a study from Chobe*
687 *National Park, Botswana*, . John Wiley & Sons.

688 Moen, A. (1999). *National atlas of Norway: Vegetation*. Norwegian Mapping Authority.

689 Myking, T., Solberg, E. J., Austrheim, G., Speed, J. D. M., Bohler, F., Astrup, R., & Eriksen,
690 R. (2013). Browsing of willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) in
691 the context of life history strategies: a literature review. *European Journal of Forest*
692 *Research*, 132, 399-409. <https://doi.org/10.1007/s10342-013-0684-3>

693 Mysterud, A. (2000). Diet overlap among ruminants in Fennoscandia. *Oecologia*, 124, 130-
694 137. <http://dx.doi.org/10.1007/s004420050032>

695 Mysterud, A., Askilrud, H., Loe, L. E., & Veiberg, V. (2010). Spatial patterns of
696 accumulated browsing and its relevance for management of red deer *Cervus elaphus*.
697 *Wildlife Biology*, 16, 162-172. <https://doi.org/10.2981/09-043>

698 Nopp-Mayr, U., Reimoser, S., Reimoser, F., Sachser, F., Obermair, L., & Gratzer, G. (2020).
699 Analyzing long-term impacts of ungulate herbivory on forest-recruitment dynamics at
700 community and species level contrasting tree densities versus maximum heights.
701 *Scientific Reports*, 10, 20274. <https://doi.org/10.1038/s41598-020-76843-3>

702 Nuttle, T., Ristau, T. E., & Royo, A. A. (2014). Long-term biological legacies of herbivore
703 density in a landscape-scale experiment: forest understoreys reflect past deer density
704 treatments for at least 20 years. *Journal of Ecology*, 102, 221-228.
705 <https://doi.org/10.1111/1365-2745.12175>

706 Palmer, S. C. F., & Truscott, A. M. (2003). Browsing by deer on naturally regenerating Scots
707 pine (*Pinus sylvestris* L.) and its effects on sapling growth. *Forest Ecology and*
708 *Management*, 182, 31-47. [https://doi.org/10.1016/s0378-1127\(03\)00026-4](https://doi.org/10.1016/s0378-1127(03)00026-4)

709 Paulsen, T. R., & Högstedt, G. (2002). Passage through bird guts increases germination rate
710 and seedling growth in *Sorbus aucuparia*. *Functional Ecology*, 16, 608-616.

711 Peláez, M., Dirzo, R., Fernandes, G. W., & Perea, R. (2019). Nurse plant size and biotic stress
712 determine quantity and quality of plant facilitation in oak savannas. *Forest Ecology*
713 *and Management*, 437, 435-442.
714 <https://doi.org/https://doi.org/10.1016/j.foreco.2019.02.010>

715 Petersson, L. K., Milberg, P., Bergstedt, J., Dahlgren, J., Felton, A. M., Götmark, F., Salk, C.,
716 & Löf, M. (2019). Changing land use and increasing abundance of deer cause natural
717 regeneration failure of oaks: Six decades of landscape-scale evidence. *Forest Ecology*
718 *and Management*, 444, 299-307.
719 <https://doi.org/https://doi.org/10.1016/j.foreco.2019.04.037>

720 Putman, R., Apollonio, M., & Andersen, R. (2011). *Ungulate management in Europe:*
721 *problems and practises*. Cambridge University Press.

722 R Development Core Team. (2020). *R: A language and environment for statistical*
723 *computing*; <http://www.R-project.org>. R Foundation for Statistical Computing.
724 <http://www.R-project.org>.

725 Ramirez, J. I., Jansen, P. A., & Poorter, L. (2018). Effects of wild ungulates on the
726 regeneration, structure and functioning of temperate forests: A semi-quantitative
727 review. *Forest Ecology and Management*, 424, 406-419.
728 <https://doi.org/https://doi.org/10.1016/j.foreco.2018.05.016>

729 Raspe, O., Findlay, C., & Jacquemart, A.-L. (2000). *Sorbus aucuparia* L. *Journal of Ecology*,
730 88, 910-930. <http://www.jstor.org/stable/2648347>

- 731 Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M.
732 W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter,
733 L. E., Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the
734 world's largest herbivores. *Science Advances*, *1*, e1400103.
735 <https://doi.org/10.1126/sciadv.1400103>
- 736 Skarpe, C., & Hester, A. (2008). Plant traits, browsing and grazing herbivores, and vegetation
737 dynamics. In I. J. Gordon & H. H. T. Prins (Eds.), *The ecology of browsing and*
738 *grazing* (pp. 217-261). Springer.
- 739 Skogen, A., & Lunde, B. L. (1997). *Flora og vegetasjon på Svanøy i Sunnfjord, med*
740 *vegetasjonskart*. Botanical Institute, University of Bergen.
- 741 Solberg, E. J., Strand, O., Veiberg, V., Andersen, R., Heim, M., Rolandsen, C. M., Langvatn,
742 R., Holmstrøm, F., Solem, M. I., Eriksen, R., Astrup, R., & Ueno, M. (2012).
743 *Hjortevilt 1991-2011: Oppsummeringsrapport fra Overvåkingsprogrammet for*
744 *hjortevilt* (NINA Rapport, Issue).
- 745 Speed, J. D. M., Austrheim, G., Kolstad, A. L., & Solberg, E. J. (2019). Long-term changes in
746 northern large-herbivore communities reveal differential rewilding rates in space and
747 time. *PLoS ONE*, *14*, e0217166. <https://doi.org/10.1371/journal.pone.0217166>
- 748 Speed, J. D. M., Meisingset, E. L., Austrheim, G., Hester, A., Mysterud, A., Tremblay, J.-P.,
749 & Solberg, E. J. (2013). Low intensities of red deer browsing constrain rowan growth
750 in mature boreal forest of western Norway. *Ecoscience*, *20*, 311-318.
- 751 Staver, A. C., & Bond, W. J. (2014). Is there a 'browse trap'? Dynamics of herbivore impacts
752 on trees and grasses in an African savanna. *Journal of Ecology*, *102*, 595-602.
753 <https://doi.org/https://doi.org/10.1111/1365-2745.12230>
- 754 Tanentzap, A. J., Kirby, K. J., & Goldberg, E. (2012). Slow responses of ecosystems to
755 reductions in deer (Cervidae) populations and strategies for achieving recovery. *Forest*
756 *Ecology and Management*, *264*, 159-166.
757 <https://doi.org/https://doi.org/10.1016/j.foreco.2011.10.005>
- 758 Thomas, P. A., El-Barghathi, M., & Polwart, A. (2007). Biological Flora of the British Isles:
759 *Juniperus communis* L. *Journal of Ecology*, *95*, 1404-1440.
760 <https://doi.org/https://doi.org/10.1111/j.1365-2745.2007.01308.x>
- 761 Tremblay, J.-P., Huot, J., & Potvin, F. (2007). Density-related effects of deer browsing on the
762 regeneration dynamics of boreal forests. *Journal of Applied Ecology*, *44*, 552-562.
763 <https://doi.org/10.1111/j.1365-2664.2007.01290.x>
- 764 Winnie, J. A. (2012). Predation risk, elk, and aspen: tests of a behaviorally mediated trophic
765 cascade in the Greater Yellowstone Ecosystem. *Ecology*, *93*, 2600-2614.
766 <https://doi.org/10.1890/11-1990.1>
767

768 Appendix A: Model verifying height as variable with high

769 explanatory value for plant size in rowan

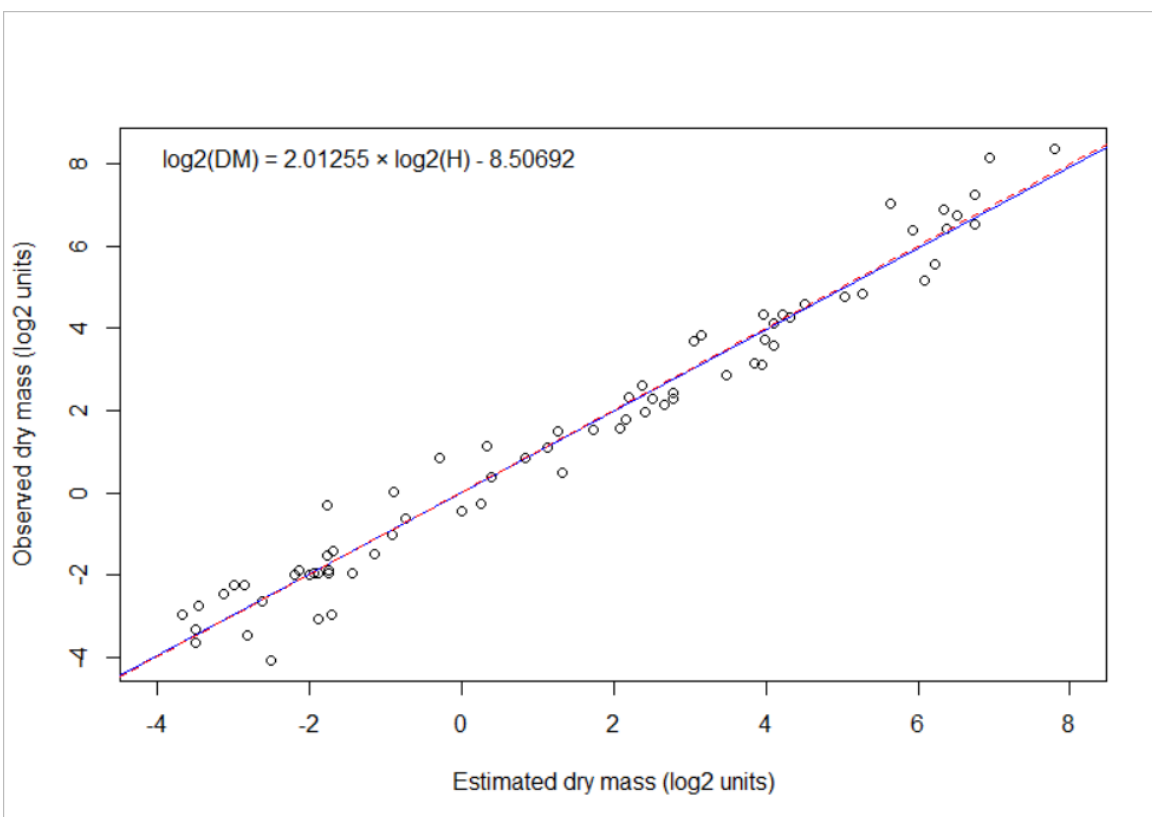
770 To test whether aboveground plant size in rowan (*Sorbus aucuparia*) was well explained by
771 measuring only plant height of saplings as we did in our study, we collected 71 rowan (*Sorbus*
772 *aucuparia*) individuals late June 2011 from the boreal forest at Svanøy. The collected

773 individuals covered a height range from 5.3 cm to 275.0 cm and were independent of the two
774 experiments detailed in the main text. None of the individuals carried flowers. On each
775 individual, we measured the height (H) and the diameter of the stem at the base (DS), counted
776 the number of leaves, measured the length of the longest leaf, and the breadth of the broadest
777 leaf, before they were dried to constant weight at 70° C in a drying cabinet. We then used a
778 GLM, with identity link and gaussian family, to build two dry mass (DM) models. One simple
779 model with only height (Fig. 1) and one more complex model with all explanatory variables
780 included. Data was log-transformed to obtain normality, and we used a forward selection
781 procedure.

782

783 The height only model had an R^2 of 0.968; $P < 0.001$: $\log_2(\text{DM}) = 2.01255 \times \log_2(\text{H}) -$

784 8.50692.



785

786 Figure 1. The relationship between estimated dry mass based on the height-model of *Sorbus*

787 *aucuparia* and the observed dry mass of the 71 individuals. The blue line is the model line,
788 whereas the red line is the 1:1 line. $R^2 = 0.968$.

789

790 The complex model included the diameter of the stem at the basis (DS) in addition to height
791 and height². This model had an R^2 of 0.989; $P < 0.001$:

792
$$\log_2(\text{DM}) = 0.55446 \times \log_2(\text{H}) + 0.06978 \times \log_2(\text{H})^2 + 1.10046 \times \log_2(\text{DS}) - 5.63338$$

793

794 As the difference in explanatory value between the height-only and the complex model was
795 negligible, and as the height-only model has a very high R^2 -value, we are confident that
796 height is a good predictor for plant size in rowan saplings.