

# Divergent roles of herbivory in eutrophying forests

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2  
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4 **Abstract**

5  
6 Ungulate herbivore populations are increasing across Europe with important implications for  
7 forest plant communities. Concurrently, atmospheric nitrogen (N) deposition continues to  
8 eutrophy forests, threatening many rare plant species. These pressures may critically interact  
9 to shape biodiversity as in grassland and tundra systems, yet any potential interactions in  
10 forests remain poorly understood. Here we combined vegetation resurveys from 52 sites in 13  
11 European countries to test how changes in ungulate herbivory and eutrophication drive long-  
12 term changes in forest understorey communities. Changes in herbivory increased temporal  
13 species turnover, however, identities of winner and loser species depended strongly on N  
14 levels. Under low level N-deposition, herbivory favored threatened and small-ranged species,  
15 while reducing non-native and nutrient-demanding species. Yet all these trends were reversed  
16 under high levels of N-deposition. Herbivores also reduced shrub cover, likely exacerbating N  
17 effects by increasing light levels in the understorey. Eutrophication levels may therefore  
18 determine whether herbivory acts as a global change catalyst for the “N time bomb”, or as a  
19 conservation tool in forests.

20  
21  
22 **Introduction**

23  
24 Temperate forests represent globally important ecosystems both as habitats supporting a  
25 unique set of species and providing essential ecosystem services<sup>1-4</sup>. These values are  
26 threatened, however, by unprecedented forest die back and loss of species diversity<sup>5-7</sup>. It is  
27 critical, therefore, to understand the processes that are beneficial or detrimental for forest  
28 functioning<sup>8</sup>. Ungulate herbivory is an important driver of ecological change in forests and  
29 populations are broadly increasing across Europe. Yet their conservation role remains highly  
30 contended<sup>9-17</sup>. Effects of herbivory are often varied and highly context dependent<sup>10</sup>, with  
31 studies rarely exploring interactions with other global change drivers. Herbivory and  
32 eutrophication have been shown to strongly interact and drive vegetation dynamics in  
33 grassland and tundra systems by mitigating light limitations and releasing low stature, often  
34 threatened, species from competition<sup>18,19</sup>. However, this interaction is poorly understood in  
35 forests where nitrogen (N) deposition often continues to exceed critical loads<sup>20-22</sup>. Examining  
36 how herbivory interacts with N-deposition in forest plant communities is, therefore, key to  
37 making informed forest management and restoration decisions.

38

39 The second half of the 20<sup>th</sup> century witnessed the resurgence of many populations of wild  
40 grazer and browser species increasing their density and range across European  
41 landscapes<sup>23,24</sup>. Several factors contributed to these trends including restrictions on hunting,  
42 hunter desires for higher game densities, land abandonment, and deliberate  
43 reintroductions<sup>25,26</sup>. Human pressures have also acted to push some of these species from  
44 more open systems into forest habitats<sup>27</sup>. Consequently, the majority of wild grazing pressure  
45 now occurs in forests with profound consequences for forest ecosystems<sup>23,28,29</sup>. Ungulate  
46 herbivores can strongly affect forest ecosystems by reducing understory vegetation biomass  
47 and tree regeneration, dispersing seeds, compacting soils, and altering rates of nutrient  
48 cycling<sup>30-32</sup>. Studies find highly heterogeneous vegetation responses to herbivory, whereby  
49 some species benefit, while others decline or disappear, in turn affecting composite indicators  
50 like plant cover and diversity<sup>9-16</sup>. Conservation effects of herbivory are yet more contentious<sup>17</sup>.  
51 Some evidence suggests that herbivory can reduce threatened species<sup>15</sup> while favouring non-  
52 natives<sup>33</sup>. Other studies find that herbivory suppresses competitive species, in turn favouring  
53 low-stature and threatened species<sup>34-36</sup>. Understanding these varying effects of herbivory is  
54 central to policy recommendations for forest and wildlife managers.

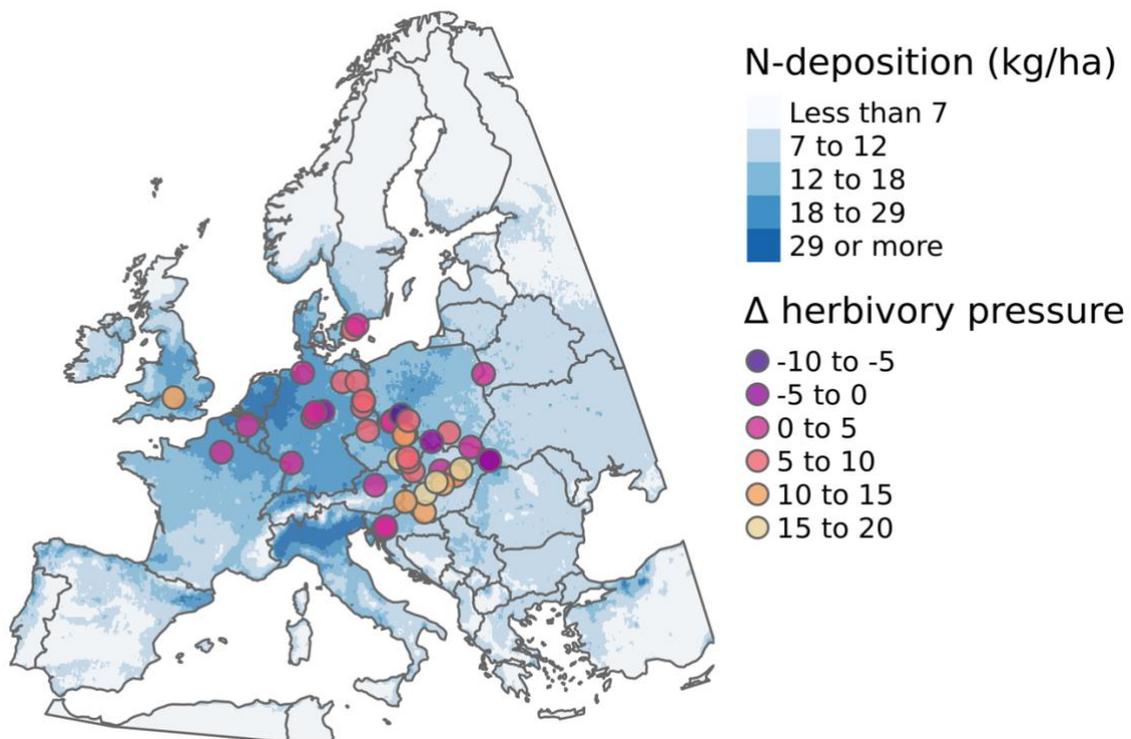
55

56 Concurrent with herbivore expansions, eutrophication of natural communities greatly  
57 increased over the last century largely in response to atmospheric N-deposition and other  
58 nutrients, as well as shifts in forest management<sup>37</sup>. This has led to the reordering of native  
59 woodland plant communities<sup>6,22</sup>. N-demanding species tend to be generalists with large  
60 climatic and geographic ranges that are most competitive in areas with high N loads. Higher  
61 growth rates allow them to outcompete N-efficient species, many of which are of low stature  
62 and/or with more restricted geographic range, traits typical of many rare and threatened  
63 species<sup>38-40</sup>. Nonetheless, experimental evidence of N additions to forest understories appear  
64 less consistent than those observed in grasslands, with forest systems remaining more stable  
65 than predicted under increasing eutrophication<sup>20-22,40-43</sup>. Shifts towards a “high forest”  
66 management system over the last century have led to average increases in the biomass of  
67 tree and/or shrub layers across many temperate European forests<sup>40,44,45</sup>. This increase is  
68 hypothesized to attenuate the impact of N-deposition by reducing light availability to the  
69 understory, generating time lags in vegetation responses<sup>7,46-48</sup>. The slow but pervasive  
70 effects of N-deposition have led some to label this threat a “N time bomb”<sup>40</sup>.

71

72 Given that large herbivores tend to reduce shrub and herb cover and height, they often  
73 increase light levels to the understory (here the herbaceous layer)<sup>49-51</sup>, thereby potentially  
74 influencing N-effects and competition among plants<sup>52,53</sup>. Here we test three alternative

75 hypotheses. (1) Increases in herbivory could alter the effects of N-deposition by mitigating light  
76 limitation and competitive effects on low-stature species as it does in grassland and tundra  
77 systems<sup>18,19,54,55</sup>; (2) as light regimes in forests differ greatly from grasslands, herbivory in  
78 forests might instead preferentially facilitate the spread of non-native, N-demanding  
79 species<sup>56,57</sup>, as these proliferate in N-enriched sites when light availability is high<sup>58</sup>; (3) there  
80 is no interactive effect of herbivory as systematic increases in canopy cover<sup>59</sup> attenuate any  
81 effect of herbivory on the shrub and understorey layers<sup>53</sup>. Our study leverages long-term  
82 vegetation data from 2928 plots in 52 resurvey studies in semi-natural temperate forest sites  
83 across Europe (median: 47.5 yrs between surveys; Figure 1) to test these hypotheses. By  
84 quantifying the interactions between herbivory and N-deposition, we add to the growing debate  
85 about whether and under what conditions herbivory can contribute to contemporary forest  
86 management at times of unprecedented environmental change.  
87

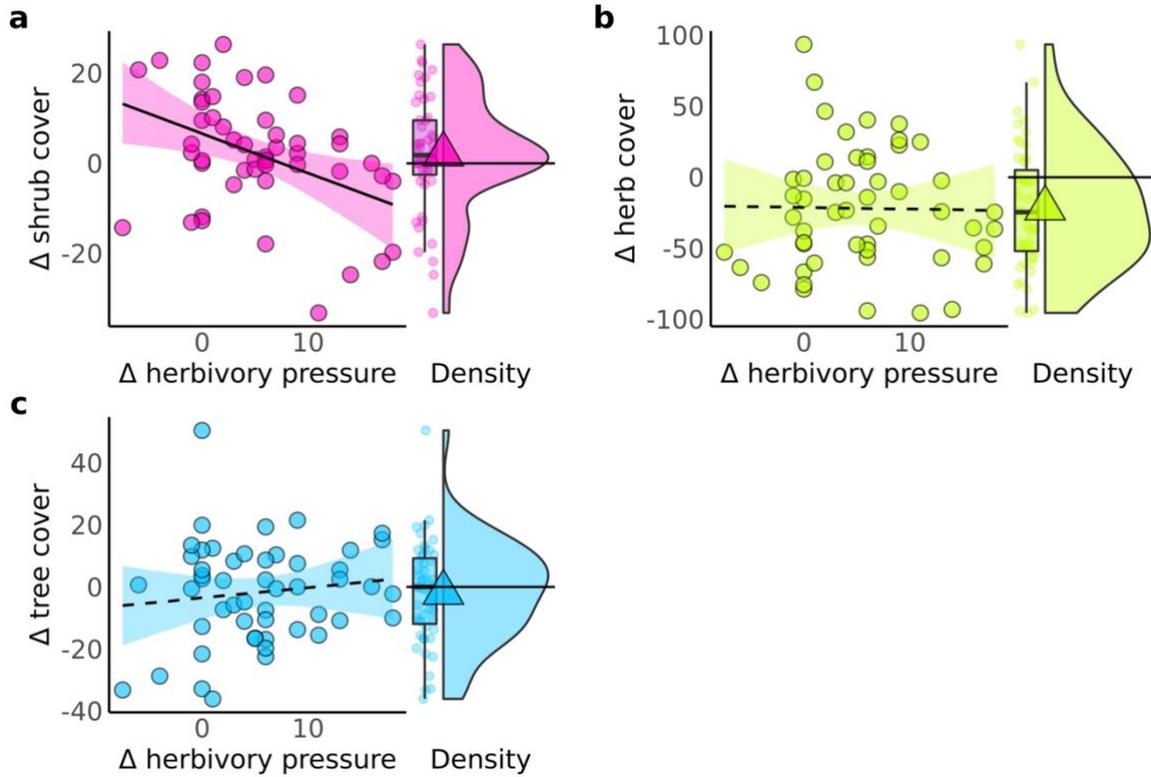


88  
89 **Fig. 1 Spatial distribution of resurvey sites, N-deposition in the year 2000, and changes**  
90 **in ( $\Delta$ ) herbivory pressure across Europe.** Map of all 52 resurvey sites (color of points  
91 correspond to the magnitude of change in site herbivore pressure between the baseline and  
92 resurvey; Table S3). Total nitrogen deposition (wet and dry, reduced and oxidized) is  
93 calculated using the EMEP database for the year 2000 and displayed across a colour gradient  
94 of light to dark blue representing lowest to highest values at a spatial resolution of 10km.  
95

96 **Results**

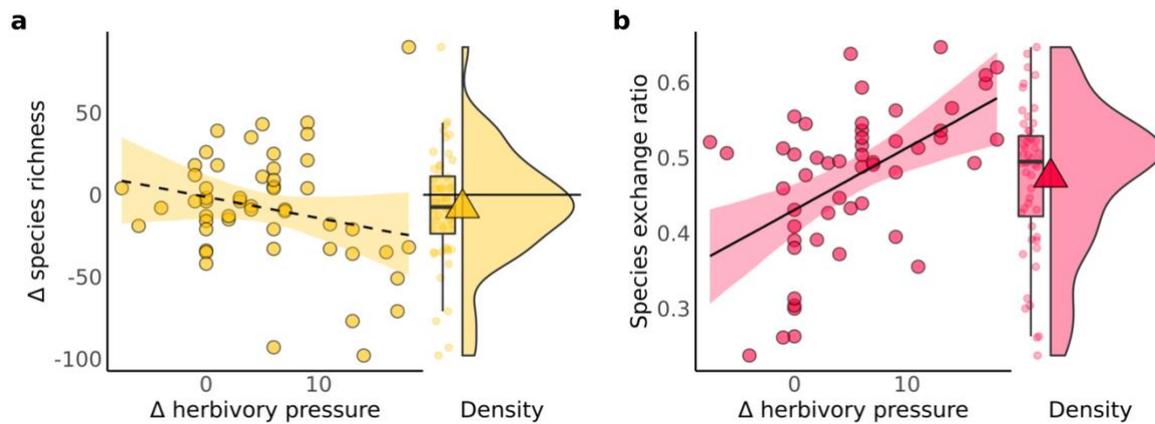
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98 We found that, on average, shrub layer cover increased, herb layer cover decreased, and tree  
 99 layer cover remained mostly constant over time in our forest sites. Increases in herbivory had  
 100 a statistically clear negative effect on shrub layer cover ( $\beta = -0.88$ ,  $\sigma = 0.34$ ), whilst the effect  
 101 on herb and tree layer cover were statistically non-discernible from zero ( $\beta = -0.12$ ,  $\sigma = 1.22$ ;  
 102  $\beta = 0.33$ ,  $\sigma = 0.47$  respectively; Figure 2a-c, Table S4-S6).  
 103



104  
 105 **Figure 2. Higher herbivory decreased shrub layer cover, but not herb and tree layer**  
 106 **cover.** Relationships between changes in ( $\Delta$ ) herbivory pressure and **a**,  $\Delta$  shrub layer cover,  
 107 **b**,  $\Delta$  herb layer cover, and **c**,  $\Delta$  tree layer cover, together with the frequency distribution  
 108 (density, boxplot and points) of the respective response variable (horizontal lines at zero  
 109 indicate no change, and triangles indicate the mean). All models included intercensal time  
 110 period, log site area, and baseline herbivory as covariates. Lines and ribbons represent the  
 111 predicted mean and its 95% credible interval, respectively. Dashed lines represent statistically  
 112 unclear relationships.  
 113

114 Herb layer species richness tended to decrease over time at the site level, but statistically it  
 115 was not clear whether herbivory contributed to this trend ( $\beta = -1.29$ ,  $\sigma = 0.95$ ; Figure 3a, Table  
 116 S7). In contrast, greater increases in herbivory clearly elevated temporal species turnover in  
 117 the herb layer ( $\beta = 0.008$ ,  $\sigma = 0.002$ ; Figure 3b, Table S8).  
 118



119

120

121 **Figure 3. Herbivory increased temporal species turnover but was not clearly associated**

122 **with changes in species richness.** Relationships between change in ( $\Delta$ ) herbivory pressure and

123 **a,  $\Delta$  species richness (number of species) and b, temporal species turnover (unitless) at**

124 **a study site, together with the frequency distribution (density, boxplot and points) of the**

125 **respective response variable (horizontal lines at zero indicate no change, and triangles**

126 **indicate the mean). All models included intercensus time period, log site area, and baseline**

127 **herbivory as covariates. Lines and ribbons represent the predicted mean and its 95% credible**

128 **interval, respectively. Dashed lines represent statistically unclear relationships.**

129

130 By testing the separate effects of herbivory and N-deposition, we found that increases in

131 herbivory shifted forest plant communities towards species with higher nutrient demands as

132 inferred from increases in community-weighted mean N-numbers (species indicator values for

133 nutrients) (CWM-N;  $\beta = 0.023$ ,  $\sigma = 0.008$ , Figure 4a, Table S9). Similarly, the proportion of

134 non-native species increased with herbivory ( $\beta = 0.164$ ,  $\sigma = 0.076$ , Figure 4c, Table S10). Per

135 contra, increases in herbivory had a negative but statistically unclear effect on the proportion

136 of species classified as threatened in national Red Lists, or of small-ranged species (Figure

137 4e and g, Table S11 and S12). To understand the relationships between herbivory, shrub

138 suppression and vegetation changes, we evaluated how changes in shrub layer cover affected

139 responses in nutrient-demanding and non-native species. Increases in shrub layer cover

140 tended to reduce both the CWM-N ( $\beta = -0.005$ ,  $\sigma = 0.003$ ) and the proportion of non-native

141 species ( $\beta = -0.082$ ,  $\sigma = 0.03$ ; Figure S1a and b, Table S13 and S14). As expected from

142 previous studies<sup>38</sup>, N-deposition reduced proportions of threatened and small-ranged species

143 ( $\beta = -0.003$ ,  $\sigma = 0.001$  and  $\beta = -0.0084$ ,  $\sigma = 0.0047$ ), but increased proportions of non-native

144 species ( $\beta = 0.006$ ,  $\sigma = 0.002$ ; Figure S2a, b and c, Table S15 – S18). Higher cumulative N-

145 deposition also tended to increase nitrophilous species, but this effect was not statistically

146 clear (Figure S2d).

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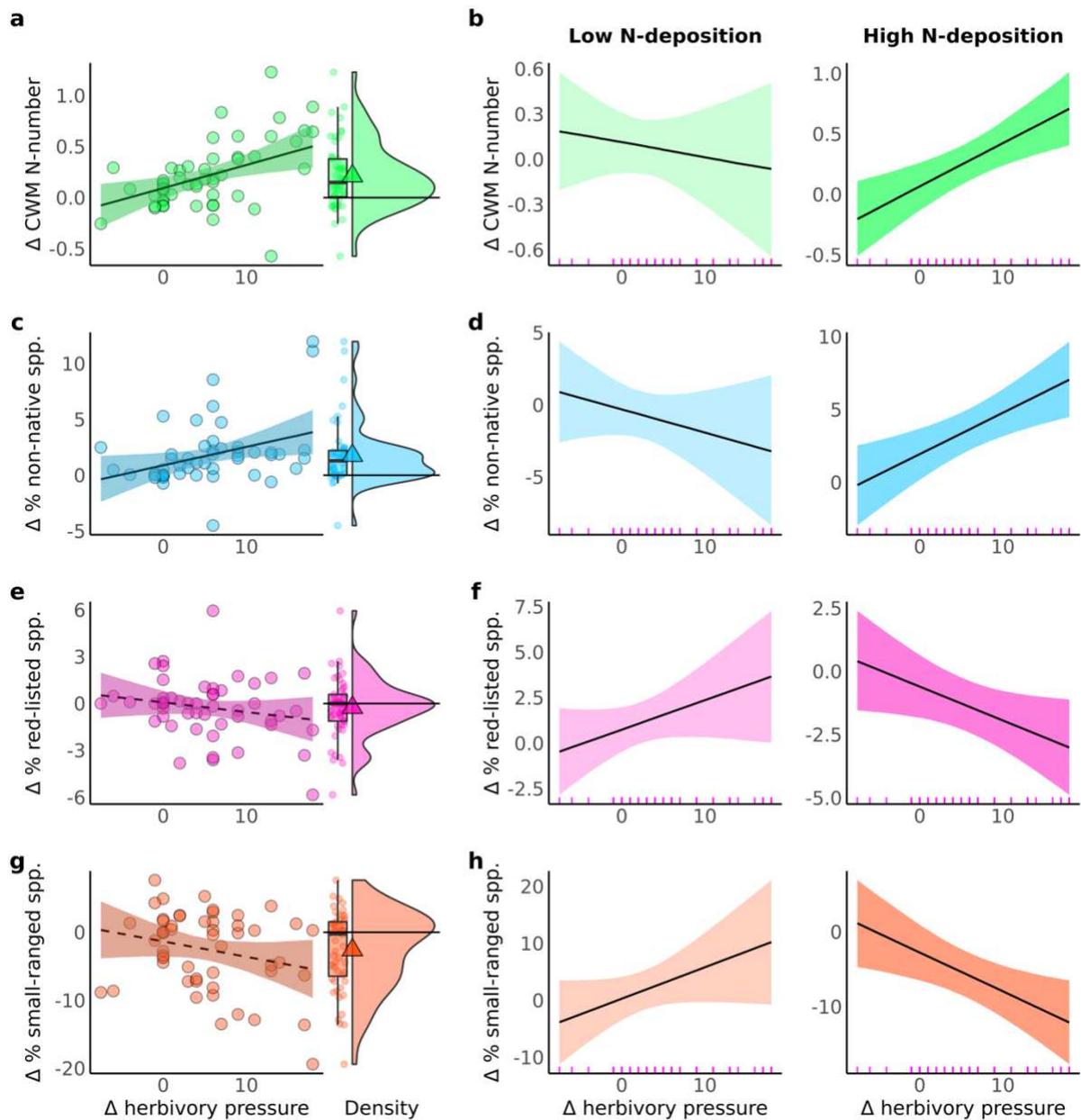
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148 **Figure 4. Herbivory effects depend on N-deposition levels.** Relationships between change in (Δ) herbivory pressure and **a**, Δ community-weighted mean N-number (CWM-N), **c**,  
 149 percentage change (Δ %) non-native species, **e**, Δ % red-listed species and **g**, Δ % small-  
 150 ranged species, together with the frequency distribution (density, boxplot and points) of the  
 151 respective response variable (horizontal lines at zero indicate no change, and triangles  
 152 indicate the mean). Herbivory effects depend on N-deposition (**b**, **d**, **f** and **h**). Conditional  
 153 effects of herbivory are depicted at the 10<sup>th</sup> (348 kg/ha; left) and 90<sup>th</sup> (1010 kg/ha; right)  
 154 percentile of cumulative N-deposition in the data. All models included intercensus time period,  
 155 log site area, and baseline herbivory as covariates. Lines and ribbons represent the predicted  
 156 mean and its 95% credible interval, respectively. Dashed lines represent statistically unclear  
 157 relationships. Rugs at figure bottom in **b**, **d**, **f** and **h** depict the marginal distribution of the  
 158 predictor. Cumulative N-deposition is calculated between the baseline and resurvey year per  
 159 site. See Figure S2 and Table S15 - 18 for model outputs of the effects of N-deposition alone.  
 160  
 161

162 Responses of all four variables to changes in herbivory not only varied but actually reversed  
 163 direction between sites subject to low vs. high levels of cumulative N-deposition (Figure 4b-h,

164 Table S19 – S22). That is, the linear trends reported above masked consistent differences in  
165 how the effects of herbivory depended on N-deposition in forest understorey communities. For  
166 example, increases in herbivory favored threatened and small-ranged species at sites subject  
167 to low cumulative N-deposition while reducing them at sites subject to high N-deposition  
168 (interaction:  $\beta = -5 \times 10^{-4}$ ,  $\sigma = 2 \times 10^{-4}$  and  $\beta = -1.6 \times 10^{-3}$ ,  $\sigma = 7 \times 10^{-4}$ , respectively; Figures 4f and  
169 h). Similarly, increases in herbivory discouraged non-native species at low N-deposition sites  
170 while increasing their proportions at high N-deposition sites (interaction:  $\beta = 7 \times 10^{-4}$ ,  $\sigma = 3 \times 10^{-4}$ ;  
171 Figure 4d). We also found that the overall effect of increased herbivory on nitrophilous  
172 species (Figure 4a) obscured the stronger effects of herbivory that occurred at high and low  
173 levels of N-deposition ( $\beta = 1 \times 10^{-4}$ ,  $\sigma = 3 \times 10^{-5}$ ). At sites with low cumulative N-deposition,  
174 increases in herbivory reduced CWM N-numbers while increased herbivory at sites with high  
175 cumulative N-deposition yielded conspicuous increases in community N-numbers (Figure 4b).  
176 In sum, the actual effects of herbivory appeared to depend on levels of N-deposition.

177

## 178 **Discussion**

179

180 Long-term data from 52 forest sites across Europe provided a natural experiment that allowed  
181 us to assess the separate and combined effects of herbivory and eutrophication on changes  
182 in forest understorey composition. Specifically, we were able to test how shifts in herbivory  
183 and N-deposition interact to affect community composition. Herbivory did not mitigate the  
184 negative effects of eutrophication as found in grasslands<sup>19,54,55</sup>. Instead, it played divergent  
185 roles in forests that depended on historical accumulated nitrogen inputs (Figure 4). At high  
186 cumulative N-deposition, increased herbivory favored nitrophilous and non-native species  
187 while diminishing species of conservation concern. Conversely, at low cumulative N-  
188 deposition, herbivory reduced nitrophilous and non-native species while favoring species of  
189 conservation concern. These results suggest that herbivory can amplify the deleterious effects  
190 of terrestrial eutrophication in forests, despite providing conservation benefits when nutrient  
191 inputs are low. These contrasting, context-dependent roles of herbivory echo and help to  
192 account for the reported heterogeneous effects of herbivory on forest community  
193 composition<sup>26</sup>. Our findings are further consistent with the hypothesis of a “N time bomb” in  
194 forests that may be triggered by disturbances that increase light availability, such as herbivory.

195

196 Herbivory may increase light availability and act on vegetation dynamics in several ways.  
197 Although shrub layer cover tended to increase at the sites of our study, herbivory reduced it  
198 (Figure 2a). This finding is consistent with other studies showing that herbivory can reduce the  
199 density and volume of woody vegetation<sup>33,50,60</sup>. Changes in tree canopy cover, however, were  
200 not associated with changes in herbivory and we found no directional change in canopy cover

201 (Figure 2c). Effects of herbivory on light availability and vegetation dynamics, thus do not  
202 appear to be fully explained by any systematic change in canopy cover. Herbivores may also  
203 reduce herbaceous plant height<sup>49,61</sup> by feeding preferentially on palatable (often nutrient-  
204 demanding) species<sup>33</sup> thereby increasing light availability and releasing space for colonizers.  
205 While we could not directly test this, we found that overall declines in herb layer cover were  
206 not associated with changes in herbivory (Figure 2b). This could also explain the negligible  
207 effect of herbivory on species richness (Figure 3a), as changes in abundance are typically  
208 accompanied by changes in species richness<sup>62,63</sup>. Nonetheless herbivory accelerated  
209 temporal turnover (Figure 3b). This may be partially explained by increased light availability  
210 following reductions of shrubby vegetation (Figure S1). Moreover, herbivores may directly alter  
211 community composition via browsing, grazing and rooting<sup>33,64</sup> as well as zoochorous seed  
212 dispersal<sup>32,65</sup>, reducing some species and enhancing propagule pressure and colonization of  
213 others. Which species benefit precisely from these processes likely depends on additional  
214 factors, such as available ambient N.

215

216 Effects of N-deposition are hypothesized to be more attenuated in forests due to low light  
217 conditions<sup>49,66</sup>. Consequently, a release of light limitations by herbivory may catalyze the  
218 spread of non-native and nitrophilous species, which often require open and disturbed sites<sup>67</sup>.  
219 Elevated ambient N-levels favor species with high growth and reproductive rates allowing  
220 them to outcompete species with more conservative growth strategies<sup>68</sup>. Outcompeted  
221 species may preferentially have conservation value – threatened and native species generally  
222 had lower N-numbers than non-threatened and non-native species (Figure S4). In contrast,  
223 sites with low N-deposition showed increases in small-ranged and threatened species, with  
224 concomitant declines in non-native, nutrient-demanding species as herbivory increased. This  
225 finding echoes studies showing that without eutrophication, herbivory favors low-stature, light-  
226 demanding herbs, many of which have lower N-demands<sup>15,69</sup>. This pattern may reflect how  
227 herbivores tend to feed on palatable species with high leaf N and reduced toxicity and perhaps  
228 that these species cannot recover as readily from herbivory when N is limited<sup>70</sup>.

229

230 Studies of herbivory effects typically rely on short-term comparisons involving artificial  
231 herbivore exclosure/enclosure sites e.g., ref.<sup>64</sup>. Our study instead leveraged data across a  
232 broad spatio-temporal scale to emphasize ecological realism with wild plant communities and  
233 free roaming herbivores (Table S3). Nevertheless, our observational approach has limitations.  
234 Our approach cannot account for all the potentially important confounding variables (or test  
235 for potential higher-order interactions among them). For example, although we did not find a  
236 statistically clear effect of site productivity here (Table S26), it would be useful to explore  
237 whether the interaction effects we observed would hold across larger productivity gradients.

238 Furthermore, our dataset reflected the natural dominance of red, roe and fallow deer and wild  
239 boar species in Europe (Table S3). These species can have different feeding preferences,  
240 physiologies, and biomass requirements to the larger feeders such as bison and moose<sup>71</sup> that  
241 were only present in a few sites. Our results are likely to be driven by these dominant species,  
242 making it essential to understand whether the observed relationships would hold should  
243 populations of other herbivores increase. Finally, our herbivore densities reflect expert local  
244 knowledge, subject to uncertainty and error, particularly for the baseline surveys. More precise  
245 experimental approaches will be useful to substantiate our findings, however these may  
246 realistically not be able to match the spatio-temporal scales of our study.

247

248 As ungulate herbivory broadly increases across Europe and N-deposition often continues to  
249 exceed critical loads<sup>24,38</sup>, our study demonstrates that herbivory and N-deposition can interact  
250 to affect forest ecosystems. Effects of herbivory depended strongly on levels of forest  
251 eutrophication for all of the key indicators we examined. These interacting effects have  
252 important implications for conservation, and especially rewilding efforts that focus on the  
253 reintroduction of herbivores in forest settings. Despite recent efforts to curtail N-emissions,  
254 rates continue to exceed critical loads in many areas with potential legacy effects on  
255 communities in the future<sup>42,72</sup>. The ability of N-demanding and many non-native species to  
256 outcompete and displace rarer and more range-limited species of conservation concern are  
257 likely to amplify and sustain such legacy effects. Therefore, policies that effectively curtail N-  
258 emissions are essential for forest protection in the long run. Depending on our ability to do so,  
259 herbivory can act either to trigger the N time bomb or as a tool to bolster species of  
260 conservation concern in the future.

261

## 262 **Methods**

263

264 **Database.** We compiled baseline vegetation survey and resurvey data from 52 sites with  
265 associated herbivory data distributed across 13 European countries in the temperate  
266 deciduous forest biome (Figure 1; see [www.forestreplot.ugent.be](http://www.forestreplot.ugent.be) and ref.<sup>40</sup> for inclusion  
267 criteria; Table S1 and S2). These sites occur in historically continuously forested natural and  
268 seminatural forest that have not experienced any substantial change in land-use either prior  
269 to the baseline survey or between the two surveys (sensu ref.<sup>73</sup>). Site areas ranged from 5.5  
270 ha to  $2.5 \times 10^6$  ha (median: 2300ha). At each site, researchers surveyed both the understorey  
271 and woody species across 10 to 190 permanent or quasi-permanent plots per site (median:  
272 50; total: 2928). Time intervals between the first and last surveys ranged from 10 to 64 years  
273 (median: 47.5 years). We accounted for changes in species taxonomy between surveys and  
274 sites by harmonizing species names following GBIF's backbone taxonomy<sup>74,75</sup>. This prevented

275 double-counting species or inferring inflated estimates of turnover. Altogether, our dataset  
276 contains 1,257 species across all sites and time periods.

277

## 278 **Explanatory variables**

279 **Herbivore pressure.** We quantified ungulate herbivore pressure at the level of a study site  
280 for the baseline and last resurvey time points based on expert assessment from each local  
281 dataset custodian/site manager in the forestREplot network<sup>18</sup>. Experts estimated herbivore  
282 densities independently per species of ungulate as the number of individuals per 100 ha on  
283 an ordinal scale from 0 (no herbivores present) to 6 (>100 individuals per 100 ha). In total  
284 there were 13 ungulate species across all sites, ranging from roe deer to European bison. We  
285 also consider wild boar as herbivore species here, even though their diet extends beyond  
286 vegetation. We then summed these ordinal values across species at each site and time period,  
287 to reflect the overall herbivore pressure, following a similar approach as in ref.<sup>8,18,76</sup> (see Table  
288 S3 for all herbivore data and full ordinal list). We then measured the equivalents of basal  
289 metabolic rates by summing the mean body mass of each species present in a site and  
290 multiplying this by the species ordinal value per site. Mean body mass per species was taken  
291 from the Phylacine database<sup>77</sup>. As these correlated highly with the density values ( $R = 0.82$ ;  
292 Fig. S4a) and given an extreme outlier of one site ( $R = 0.92$  when this outlier was removed,  
293 Fig. S4b), we used our herbivore pressure index above in all analyses to avoid leverage.  
294 Temporal herbivore pressure was calculated as the difference between the last resurvey and  
295 the baseline survey values per study site<sup>18</sup>, with index values ranging from -8 to 18 (Figure 1,  
296 S5a and Table S3).

297

298 **N-deposition.** We quantified total cumulative N-deposition using the EMEP database  
299 ([https://emep.int/mscw/mscw\\_moddata.html](https://emep.int/mscw/mscw_moddata.html)), using cumulative wet and dry deposition of  
300 oxidized and reduced nitrogen<sup>78</sup>. We calculated the cumulative N-deposition between the  
301 baseline year and the year of the resurvey based on the methods described in ref.<sup>8</sup>. Therefore,  
302 cumulative N-deposition per site will be influenced by the rate of deposition per year, as well  
303 as the length of the intercensal intervals (i.e., sites with lower yearly rates but long intervals  
304 may have similar values to sites with high yearly rates but shorter intervals). The values of  
305 cumulative N-deposition ranged from 130 to 1296 kg ha<sup>-1</sup> (Figure S5b and Table S2).

306

307 **Site productivity.** To control for the potentially confounding influence of productivity on  
308 vegetation responses to herbivory<sup>79,80</sup>, we obtained local environmental data from the  
309 EuMedClim database<sup>81</sup> on both the potential evapotranspiration and annual precipitation for  
310 each site averaged across the baseline and resurvey years. We then calculated the annual  
311 precipitation to potential evapotranspiration ratio (AP:PET) as a productivity proxy metric<sup>82</sup>.

312 The EuMedClim database ranges from 1901 – 2014 so any sites that had been resurveyed  
313 since 2014 were given the 2014 value as their resurvey value. We calculated the average of  
314 the two time points. AP:PET values ranged from 0.58 – 2.1 across sites.

315

### 316 **Response variables**

317 **Herb, shrub, and tree cover.** We estimated the cover values of the herb (here defined as all  
318 vascular plant species <1m), shrub (1 – 7m) and tree (>7m) layers by summing cover values  
319 over all species within each layer in a plot per site and then averaging across all the plots at  
320 each site for each variable. We estimated temporal changes in these values by subtracting  
321 the baseline value from the resurvey value<sup>8,83</sup>. Two sites lacked shrub cover data, with one of  
322 these sites also lacking herb cover data, leaving 50 and 51 sites available for study for these  
323 respective variables. The change values of the herb layer ranged from -94 to 67%, for the  
324 shrub layer the change values were -24 to 22%, and for the tree layer they were -50 to 29%.

325

326

327 **Species richness change and exchange ratios.** Species richness change was calculated  
328 as the difference of the number of herbaceous species at each site between the resurvey and  
329 baseline survey<sup>8,83</sup>. Herbaceous species turnover was estimated using richness-based  
330 species exchange ratios<sup>84</sup> calculated at the site level as:

331

$$SER_r = \frac{(S_{imm} + S_{ext})}{S_{tot}}$$

332 where  $S_{imm}$  = the number of species gained at resurvey,  $S_{ext}$  = the number of species lost at  
333 resurvey,  $S_{tot}$  = total number of unique species at baseline and resurvey. We tested for a  
334 relationship between site area and exchange ratio to account for a potential sampling bias  
335 across the sites and found no clear statistical relationship (Figure S6), however, we still  
336 included site area as a variable in the model (see below) to control for this. The range of  
337 change values for species richness and exchange ratios were -98 to 90 and 0.24 to 0.65  
338 respectively.

339

340 **Species of conservation value.** We identified species of conservation value using two  
341 criteria: (1) Species listed as threatened in national Red Lists based on a recent database  
342 synthesizing national Red Lists across Europe<sup>85</sup>. That is, we determined the threat status of  
343 each species at a given site based on the respective national Red List of the country in which  
344 that site was located (based on IUCN threat classifications, see ref.<sup>86</sup>). We then calculated the  
345 percentage of threatened species per site per survey period (baseline site mean = 2.2%,  
346 resurvey site mean = 1.9%). (2) Species that have small geographic range sizes. Our range  
347 size estimates are based on areas of occupancy (AOO, in km<sup>2</sup>) derived from point occurrence

348 records in GBIF by ref.<sup>86</sup>. We determined the lowest quintile of range size, which we classified  
349 as small ranged. We then calculated the percentage of small-ranged species at each site and  
350 survey period and used changes in these over time to quantify the temporal change (baseline  
351 site mean = 4.1%, resurvey site mean = 3.8%).

352

353 ***Non-native and nutrient-demanding species.*** We identified the non-native species present  
354 at each site using the Global Register of Introduced and Invasive Species (GRIIS;  
355 <http://www.griis.org>) and its designations of which species are non-native in each country. We  
356 then calculated the percentage of non-native species per site per survey period and the  
357 difference over time (baseline site mean = 3.0%, resurvey site mean = 4.8%). We estimated  
358 shifts in species' N demands using ecological indicator values (EIVs) compiled from ref.<sup>87</sup>  
359 ([sci.muni.cz/botany/juice/ELLENB.TXT](http://sci.muni.cz/botany/juice/ELLENB.TXT)) filling data gaps with values from ref.<sup>88</sup>. Coverage of  
360 N-numbers was 92% of species (1,156 out of 1,257 species). For each study site and survey  
361 period, we quantified the community weighted mean (CWM) N number using the baseline and  
362 resurvey weighted occupancy per species per study site and calculated their difference over  
363 time. The CWM N-number change over time ranged from -0.57 to 1.23 across sites.

364

### 365 ***Data analysis***

366 We fitted Bayesian linear models using the brms package in R for all statistical analyses. R  
367 Code and data for all analyses are available on Figshare (link will be provided if published).  
368 We controlled for site factors, i.e., total site area, time intervals between surveys and where  
369 appropriate, baseline herbivory and site productivity. For all analyses, we used the 95%  
370 credible interval to determine statistical clarity<sup>89</sup>. For brevity, only the main models are  
371 presented here (but all model syntaxes can be found on Figshare).

372

373 ***Structural changes and turnover.*** We tested whether cover values ( $r_i$ ) and metrics of  
374 diversity (species richness and exchange ratio:  $d_i$ ) changed with changes in herbivory ( $h_i$ ).  
375 We included the intercensus time period ( $t_i$ ), the site area ( $s_i$ ) and baseline herbivory ( $b_i$ ) in  
376 both models to account for response variation that might be due to these factors generating  
377 the following models where  $\alpha$  is the intercept and  $\beta$  is the slope of the predictor:

378

$$379 \quad r_i \sim \text{Normal}(\mu_i, \sigma)$$

$$380 \quad \mu_i \sim \alpha + \beta_h h_i + \beta_t t_i + \beta_s s_i + \beta_b b_i$$

381

$$382 \quad d_i \sim \text{Normal}(\mu_i, \sigma)$$

$$383 \quad \mu_i \sim \alpha + \beta_h h_i + \beta_t t_i + \beta_s s_i + \beta_b b_i$$

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**Herbivore and nitrogen effects on vegetation.** We tested for the separate effects of herbivory and N-deposition ( $n_i$ ) on species of conservation concern, non-native species, the CWM N-number ( $e_i$ ). We included the intercensus time period ( $t_i$ ), the site area ( $s_i$ ) and baseline herbivory ( $b_i$ ) to account for response variation that might be due to these factors:

$$e_i \sim \text{Normal}(\mu_i, \sigma)$$
$$\mu_i \sim \alpha + \beta_n \text{ or } h n \text{ or } h_i + \beta_t t_i + \beta_s s_i + \beta_b b_i$$

**Interaction effect.** Before being able to test interaction effects between temporal changes in herbivory pressure and N-deposition, we validated that these predictor variables were relatively independent and so satisfy our assumption that this natural experiment reflects a quasi-factorial design. Indeed, we found no significant correlation between cumulative N-deposition and changes in herbivory over time ( $\beta = 0.004$ ,  $\sigma = 0.004$ ). This allowed us to then test for interaction effects between the effects of changes in herbivory and N-deposition on our dependent variables: changes in species of conservation concern, non-native species, the CWM N-number ( $e_i$ ). We included the inter-census time period ( $t_i$ ), the site area ( $s_i$ ) and baseline herbivory ( $b_i$ ) to control for variation in the response that might be due to these factors, generating the following model:

$$e_i \sim \text{Normal}(\mu_i, \sigma)$$
$$\mu_i \sim \alpha + \beta_h h_i * \beta_n n_i + \beta_t t_i + \beta_s s_i + \beta_b b_i$$

For all models we initially tested the effect of site productivity and tree cover as covariates (Table S26 and S27). However, we did not see a statistically clear effect of these covariates for any models except on herb cover. Because they were not considered a necessary site variable to account for study design (such as site area and intercensus time periods), and to reduce the risk of model overfitting (given that we have only 52 data points), we subsequently removed these covariates from our main analyses.

## **References**

1. FAO. *Global forest resources assessment* . [www.fao.org/publications](http://www.fao.org/publications) (2015).
2. Finlayson, M. *et al.* A Report of the Millennium Ecosystem Assessment Contributing Authors, and Sub-global Coordinators Review Editors: José Sarukhán and Anne

- 421 Whyte (Co-chairs) and MA Board of Review Editors The Cropper Foundation,  
 422 Trinidad and Tobago. (2005).
- 423 3. Lal, R. & Lorenz, K. Carbon Sequestration in Temperate Forests. *Recarbonization of*  
 424 *the Biosphere: Ecosystems and the Global Carbon Cycle* 187–201 (2012)  
 425 doi:10.1007/978-94-007-4159-1\_9.
  - 426 4. Gilliam, F. S. Forest ecosystems of temperate climatic regions: from ancient use to  
 427 climate change. *New Phytologist* **212**, 871–887 (2016).
  - 428 5. de Gouvenain, R. C. & Silander, J. A. Temperate Forests ☆. in *Reference Module in*  
 429 *Life Sciences* (Elsevier, 2017). doi:10.1016/b978-0-12-809633-8.02310-4.
  - 430 6. Keith, S. A., Newton, A. C., Morecroft, M. D., Bealey, C. E. & Bullock, J. M.  
 431 Taxonomic homogenization of woodland plant communities over 70 years.  
 432 *Proceedings of the Royal Society B: Biological Sciences* **276**, 3539–3544 (2009).
  - 433 7. Rackham, O. Ancient woodlands: modern threats. *New Phytologist* **180**, 571–586  
 434 (2008).
  - 435 8. Bernhardt-Römermann, M. *et al.* Drivers of temporal changes in temperate forest plant  
 436 diversity vary across spatial scales. *Global Change Biology* **21**, 3726–3737 (2015).
  - 437 9. Waller, D. M. & Alverson, W. S. The White-Tailed Deer: A Keystone Herbivore.  
 438 *Wildlife Society Bulletin (1973-2006)* **25**, 217–226 (1997).
  - 439 10. Ramirez, J. I. Uncovering the different scales in deer–forest interactions. *Ecology and*  
 440 *Evolution* **11**, 5017–5024 (2021).
  - 441 11. Rooney, T. P., Wiegmann, S. M., Rogers, D. A. & Waller, D. M. *Biotic*  
 442 *Impoverishment and Homogenization in Unfragmented Forest Understory*  
 443 *Communities*. *Conservation Biology* vol. 18 (2004).
  - 444 12. Stockton, S. A., Allombert, S., Gaston, A. J. & Martin, J. L. A natural experiment on  
 445 the effects of high deer densities on the native flora of coastal temperate rain forests.  
 446 *Biological Conservation* **126**, 118–128 (2005).
  - 447 13. Hegland, S. J., Lilleeng, M. S. & Moe, S. R. Old-growth forest floor richness increases  
 448 with red deer herbivory intensity. *Forest Ecology and Management* **310**, 267–274  
 449 (2013).
  - 450 14. Simončič, T., Bončina, A., Jarni, K. & Klopčič, M. Assessment of the long-term  
 451 impact of deer on understory vegetation in mixed temperate forests. *Journal of*  
 452 *Vegetation Science* **30**, 108–120 (2019).
  - 453 15. Vild, O. *et al.* The paradox of long-term ungulate impact: increase of plant species  
 454 richness in a temperate forest. *Applied Vegetation Science* **20**, 282–292 (2017).
  - 455 16. Russell, F. L., Zippin, D. B. & Fowler, N. L. Effects of White-tailed Deer (*Odocoileus*  
 456 *virginianus*) on Plants, Plant Populations and Communities: A Review. *The American*  
 457 *Midland Naturalist* **146**, 1–26 (2001).
  - 458 17. Öllerer, K. *et al.* Beyond the obvious impact of domestic livestock grazing on  
 459 temperate forest vegetation—A global review. *Biological Conservation* **237**, 209–219  
 460 (2019).
  - 461 18. Borer, E. T. *et al.* Nutrients cause grassland biomass to outpace herbivory. *Nature*  
 462 *Communications* **11**, 1–8 (2020).
  - 463 19. Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. Herbivores rescue diversity in warming  
 464 tundra by modulating trait-dependent species losses and gains. *Nature*  
 465 *Communications* **2017** 8:1 **8**, 1–8 (2017).
  - 466 20. Simkin, S. M. *et al.* Conditional vulnerability of plant diversity to Atmospheric  
 467 nitrogen deposition across the United States. *Proc Natl Acad Sci U S A* **113**, 4086–  
 468 4091 (2016).
  - 469 21. Bobbink, R. *et al.* Global assessment of nitrogen deposition effects on terrestrial plant  
 470 diversity: A synthesis. *Ecological Applications* **20**, 30–59 (2010).

- 471 22. Reinecke, J., Klemm, G. & Heinken, T. Vegetation change and homogenization of  
472 species composition in temperate nutrient deficient Scots pine forests after 45 yr.  
473 *Journal of Vegetation Science* **25**, 113–121 (2014).
- 474 23. Speed, J. D. M., Austrheim, G., Kolstad, A. L. & Solberg, E. J. Long-term changes in  
475 northern large-herbivore communities reveal differential rewilding rates in space and  
476 time. *PLOS ONE* **14**, e0217166 (2019).
- 477 24. Valente, A. M., Acevedo, P., Figueiredo, A. M., Fonseca, C. & Torres, R. T.  
478 Overabundant wild ungulate populations in Europe: management with consideration of  
479 socio-ecological consequences. *Mammal Review* **50**, 353–366 (2020).
- 480 25. Linnell, J. D. C. *et al.* The challenges and opportunities of coexisting with wild  
481 ungulates in the human-dominated landscapes of Europe’s Anthropocene. *Biological*  
482 *Conservation* vol. 244 108500 (2020).
- 483 26. Waller D.M. 2014. Effects of deer on forest herb layers. Chapter 16, pp. 369-399, In:  
484 FS Gilliam, editor. *The herbaceous layer in forests of Eastern North America*,  
485 2<sup>nd</sup> edition. New York, NY: Oxford University Press, Inc.
- 486 27. Kerley, G. I. H., Kowalczyk, R. & Cromsigt, J. P. G. M. Conservation implications of  
487 the refugee species concept and the European bison: king of the forest or refugee in a  
488 marginal habitat? (2011).
- 489 28. Svenning, J. C. A review of natural vegetation openness in north-western Europe.  
490 *Biological Conservation* **104**, 133–148 (2002).
- 491 29. Sandom, C. J., Ejrnaes, R., Hansen, M. D. D. & Svenning, J. C. High herbivore density  
492 associated with vegetation diversity in interglacial ecosystems. *Proc Natl Acad Sci U S*  
493 *A* **111**, 4162–4167 (2014).
- 494 30. Ramirez, J. I., Jansen, P. A., den Ouden, J., Goudzwaard, L. & Poorter, L. Long-term  
495 effects of wild ungulates on the structure, composition and succession of temperate  
496 forests. *Forest Ecology and Management* **432**, 478–488 (2019).
- 497 31. Ramirez, J. I., Jansen, P. A. & Poorter, L. Effects of wild ungulates on the  
498 regeneration, structure and functioning of temperate forests: A semi-quantitative  
499 review. *Forest Ecology and Management* **424**, 406–419 (2018).
- 500 32. Albert, A. *et al.* Seed dispersal by ungulates as an ecological filter: a trait-based meta-  
501 analysis. *Oikos* **124**, 1109–1120 (2015).
- 502 33. Boulanger, V. *et al.* Ungulates increase forest plant species richness to the benefit of  
503 non-forest specialists. *Global Change Biology* **24**, e485–e495 (2018).
- 504 34. Kirby, K. J. The impact of deer on the ground flora of British broadleaved woodland.  
505 *Forestry: An International Journal of Forest Research* **74**, 219–229 (2001).
- 506 35. Royo, A. A., Collins, R., Adams, M. B., Kirschbaum, C. & Carson, W. P. Pervasive  
507 interactions between ungulate browsers and disturbance regimes promote temperate  
508 forest herbaceous diversity. *Ecology* **91** (2010).
- 509 36. Happonen, K. *et al.* Trait-based responses to land use and canopy dynamics modify  
510 long-term diversity changes in forest understories. *Global Ecology and Biogeography*  
511 **30**, 1863–1875 (2021).
- 512 37. Peñuelas, J. & Sardans, J. The global nitrogen-phosphorus imbalance. *Science (1979)*  
513 **375**, 266–267 (2022).
- 514 38. Staude, I. R. *et al.* Replacements of small- by large-ranged species scale up to diversity  
515 loss in Europe’s temperate forest biome. *Nature Ecology and Evolution* **4**, 802–808  
516 (2020).
- 517 39. Newbold, T. *et al.* Widespread winners and narrow-ranged losers: Land use  
518 homogenizes biodiversity in local assemblages worldwide. *PLOS Biology* **16**,  
519 e2006841 (2018).

- 520 40. Verheyen, K. *et al.* Driving factors behind the eutrophication signal in understorey  
521 plant communities of deciduous temperate forests. *British Ecological Society Journal*  
522 *of Ecology* **100**, 352–365 (2012).
- 523 41. Gilliam, F. S. Response of the herbaceous layer of forest ecosystems to excess nitrogen  
524 deposition. *Journal of Ecology* **94**, 1176–1191 (2006).
- 525 42. de Schrijver, A. *et al.* Cumulative nitrogen input drives species loss in terrestrial  
526 ecosystems. doi:10.1111/j.1466-8238.2011.00652.x.
- 527 43. de Frenne, P. *et al.* Light accelerates plant responses to warming. *Nature Plants* **1**,  
528 15110 (2015).
- 529 44. Baeten, L. *et al.* Herb layer changes (1954–2000) related to the conversion of coppice-  
530 with-standards forest and soil acidification. *Applied Vegetation Science* **12**, 187–197  
531 (2009).
- 532 45. Becker, T., Spanka, J., Schröder, L. & Leuschner, C. Forty years of vegetation change  
533 in former coppice-with-standards woodlands as a result of management change and N  
534 deposition. *Applied Vegetation Science* **20**, 304–313 (2017).
- 535 46. van Calster, H. *et al.* Diverging effects of overstorey conversion scenarios on the  
536 understorey vegetation in a former coppice-with-standards forest. *Forest Ecology and*  
537 *Management* **256**, 519–528 (2008).
- 538 47. Luysaert, S. *et al.* The European carbon balance. Part 3: forests. *Global Change*  
539 *Biology* **16**, 1429–1450 (2010).
- 540 48. Kirby, K. J. *et al.* Five decades of ground flora changes in a temperate forest: The  
541 good, the bad and the ambiguous in biodiversity terms. *Forest Ecology and*  
542 *Management* **505**, 119896 (2022).
- 543 49. Hautier, Y., Niklaus, P. A. & Hector, A. Competition for light causes plant  
544 biodiversity loss after eutrophication. *Science (1979)* **324**, 636–638 (2009).
- 545 50. Kowalczyk, R., Kamiński, T. & Borowik, T. Do large herbivores maintain open  
546 habitats in temperate forests? *Forest Ecology and Management* **494**, (2021).
- 547 51. Dormann, C. F. *et al.* Plant species richness increases with light availability, but not  
548 variability, in temperate forests understorey. *BMC Ecology* **20**, 1–9 (2020).
- 549 52. Dirnböck, T. *et al.* Forest floor vegetation response to nitrogen deposition in Europe.  
550 *Global Change Biology* **20**, 429–440 (2014).
- 551 53. Perring, M. P. *et al.* Understanding context dependency in the response of forest  
552 understorey plant communities to nitrogen deposition. *Environmental Pollution* **242**,  
553 1787–1799 (2018).
- 554 54. Anderson, T. M. *et al.* Herbivory and eutrophication mediate grassland plant nutrient  
555 responses across a global climatic gradient. *Ecology* **99**, 822–831 (2018).
- 556 55. Gough, L. & Grace, J. B. Herbivore effects on plant species density at varying  
557 productivity levels. *Ecology* **79**, 1586–1594 (1998).
- 558 56. Knight, T. M., Dunn, J. L., Smith, L. A., Davis, J. A. & Kalisz, S. Deer Facilitate  
559 Invasive Plant Success in a Pennsylvania Forest Understorey. *Natural Areas* **29**, 110–  
560 116 (2009).
- 561 57. Beguin, J., Pothier, D. & Côté, S. D. Deer browsing and soil disturbance induce  
562 cascading effects on plant communities: a multilevel path analysis. *Ecological*  
563 *Applications* **21** (2011).
- 564 58. Gilliam, F. S. *et al.* Twenty-five-year response of the herbaceous layer of a temperate  
565 hardwood forest to elevated nitrogen deposition. *Ecosphere* **7**, e01250 (2016).
- 566 59. de Frenne, P. *et al.* Microclimate moderates plant responses to macroclimate warming.  
567 *Proc Natl Acad Sci U S A* **110**, 18561–18565 (2013).
- 568 60. Boulanger, V. *et al.* Decreasing deer browsing pressure influenced understorey  
569 vegetation dynamics over 30 years. *Annals of Forest Science* **72**, 367–378 (2015).

- 570 61. Rooney, T. P. & Waller, D. M. Direct and indirect effects of white-tailed deer in forest  
571 ecosystems. **1127** (2003).
- 572 62. Storch, D., Bohdalková, E. & Okie, J. The more-individuals hypothesis revisited: the  
573 role of community abundance in species richness regulation and the productivity–  
574 diversity relationship. *Ecology Letters* **21**, 920–937 (2018).
- 575 63. Srivastava, D. S. & Lawton, J. H. Why More Productive Sites Have More Species: An  
576 Experimental Test of Theory Using Tree-Hole Communities. **152**, 510–529 (2015).
- 577 64. Bernes, C. *et al.* Manipulating ungulate herbivory in temperate and boreal forests:  
578 Effects on vegetation and invertebrates. A systematic review. *Environmental Evidence*  
579 **7**, 1–32 (2018).
- 580 65. Vavra, M., Parks, C. G. & Wisdom, M. J. Biodiversity, exotic plant species, and  
581 herbivory: The good, the bad, and the ungulate. *Forest Ecology and Management* **246**,  
582 66–72 (2007).
- 583 66. Depauw, L. *et al.* Light availability and land-use history drive biodiversity and  
584 functional changes in forest herb layer communities. *Journal of Ecology* **108**, 1411–  
585 1425 (2020).
- 586 67. de Pauw, K. *et al.* Forest understorey communities respond strongly to light in  
587 interaction with forest structure, but not to microclimate warming. *New Phytologist*  
588 **233**, 219–235 (2022).
- 589 68. Clark, C. M. *et al.* Potential vulnerability of 348 herbaceous species to atmospheric  
590 deposition of nitrogen and sulfur in the United States. *Nat. Plants* **5**, 697–705 (2019).
- 591 69. Chevaux, L. *et al.* Effects of stand structure and ungulates on understory vegetation in  
592 managed and unmanaged forests. *Ecological Applications* **32** (2022).
- 593 70. Hawkes, C. v & Sullivan, J. J. The impact of herbivory on plants in different resource  
594 conditions: a meta-analysis. *Ecology* **82**, 2045–2058 (2001).
- 595 71. Gordon, I. J. Browsing and grazing ruminants: are they different beasts? *Forest*  
596 *Ecology and Management* **181**, 13–21 (2003).
- 597 72. Brasseur, B. *et al.* What deep-soil profiles can teach us on deep-time pH dynamics  
598 after land use change? *Land Degradation & Development* **29**, 2951–2961 (2018).
- 599 73. Peterken, G. F. *Natural woodland: ecology and conservation in northern temperate*  
600 *regions*. (Cambridge university press, 1996).
- 601 74. Chamberlain, S. A. & Boettiger, C. R Python, and Ruby clients for GBIF species  
602 occurrence data. preprint. PeerJ Preprints. (2017).
- 603 75. Chamberlain, S. A. & Szöcs, E. taxize: taxonomic search and retrieval in R. *F1000Res*  
604 **2**, 191 (2013).
- 605 76. Andersen, R. *et al.* An overview of the progress and challenges of peatland restoration  
606 in Western Europe. *Restoration Ecology* **25**, 271–282 (2017).
- 607 77. Faurby, S. *et al.* PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology.  
608 *Ecology* **99**, 2626 (2018).
- 609 78. van den Berg, L. J. L. *et al.* Evidence for differential effects of reduced and oxidised  
610 nitrogen deposition on vegetation independent of nitrogen load. *Environmental*  
611 *Pollution* **208**, 890–897 (2016).
- 612 79. McNaughton, S. J., Oesterheld, M., Frank, D. A. & Williams, K. J. Ecosystem-level  
613 patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341**, 142–  
614 144 (1989).
- 615 80. Koerner, S. E. *et al.* Change in dominance determines herbivore effects on plant  
616 biodiversity. *Nature Ecology and Evolution* **2**, 1925–1932 (2018).
- 617 81. Fréjaville, T. & Garzón, M. B. The EuMedClim database: Yearly climate data (1901–  
618 2014) of 1 km resolution grids for Europe and the Mediterranean Basin. *Frontiers in*  
619 *Ecology and Evolution* **6**, 1–5 (2018).

- 620 82. Al-Yaari, A. *et al.* Asymmetric responses of ecosystem productivity to rainfall  
621 anomalies vary inversely with mean annual rainfall over the conterminous United  
622 States. *Global Change Biology* **26**, 6959–6973 (2020).
- 623 83. Hedges, L. v, Gurevitch, J. & Curtis, P. S. The meta-analysis of response ratios in  
624 experimental ecology. *Special Feature Ecology* **80**, 1150–1156 (1999).
- 625 84. Hillebrand, H. *et al.* Biodiversity change is uncoupled from species richness trends:  
626 Consequences for conservation and monitoring. *Journal of Applied Ecology* **55**, 169–  
627 184 (2018).
- 628 85. Holz, H., Segar, J., Valdez, J. & Staude, I. R. Assessing extinction risk across the  
629 geographic ranges of plant species in Europe. *Plants, People, Planet* (2022)
- 630 86. Staude, I. R. *et al.* Directional turnover towards larger-ranged plants over time and  
631 across habitats. *Ecology Letters* (2021).
- 632 87. Ellenberg, H. , Weber, H. E. , Düll, R. , Wirth, V. & Werner, W. Zeigerwerte von  
633 Pflanzen in Mitteleuropa. *Goltze* (2001).
- 634 88. Chytrý, M., Tichý, L., Dřevojan, P., Sádlo, J. & Zelený, D. Ellenbergtype indicator  
635 values for the Czech flora. (2018).
- 636 89. Dushoff, J., Kain, M. P. & Bolker, B. M. I can see clearly now: Reinterpreting  
637 statistical significance. *Methods in Ecology and Evolution* **10**, 756–759 (2019).
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