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1 **A comparison of clearfelling and gradual thinning of plantations for**
2 **the restoration of insect herbivores and woodland plants**

3

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12

13 **Running title:** Comparing plantation clearfelling and thinning

14

15

16 **Summary**

17

18 **1.** Testing restoration methods is essential for the development of restoration ecology
19 as a science. It is also important to monitor a range of taxa, not just plants which have
20 been the traditional focus of restoration ecology. Here we compare the effects on
21 ground flora and leaf-miners, of two restoration practices used when restoring conifer
22 plantations.

23

24 **2.** Two methods of restoration were investigated: clearfelling of plantations and the
25 gradual thinning of conifers over time. Unrestored plantations and native broad-
26 leaved woodlands were also surveyed, these representing the starting point of
27 restoration and the reference community respectively. The study sites consist of two
28 forest types (acidic *Quercus* woodland and mesotrophic *Fraxinus* woodland) enabling
29 us to compare the two restoration methods in different habitat types. We use a well-
30 replicated, large-scale study system consisting of 32 woodland plots, each 2 ha in size.

31

32 **3.** There were 179 plant species identified in the plots. Clearfelled plots had greater
33 overall ground flora species richness than other management regimes (thinned,
34 unrestored plantation and native woodland), but the richness of woodland plant
35 species did not differ between clearfelled, thinned, native woodland and unrestored
36 plantation plots.

37

38 **4.** More than 10 000 leaf-miners comprising 122 species were collected. Increased
39 plant species richness was associated with increased leaf-miner species richness under
40 all management regimes except clearfelled plots.

41

42 **5.** Forest type did not affect the response to restoration method, i.e. there was no
43 interaction between management regime and forest type for any of the variables
44 measured.

45

46 **6. *Synthesis and applications.*** Our results suggest that both the clearfelling and
47 gradual thinning approaches to plantation restoration maintain woodland ground flora
48 species. Either method can be used without detriment to woodland ground flora
49 species richness. However, these methods differed in their effects on the leaf-miner–
50 plant species richness relationship. If increasing invertebrate herbivore species
51 richness is a concern the gradual thinning approach is more appropriate.

52

53 **Key-words:** Ancient woodland, ground flora, herbaceous layer, herbivore
54 community, leaf-miners, PAWS, plant community, plantation management, species
55 richness

56 **Introduction**

57 Ecological restoration is essential for creating resilient ecological networks, ensuring
58 sustainable provision of ecosystem services, and conserving threatened species and
59 habitats (Young 2000; Hobbs & Harris 2001; Lawton *et al.* 2010). The restoration of
60 degraded forests is taking place across the globe, and although forests vary in
61 structure and species composition, similar methods are used for forest restoration
62 worldwide (Stanturf, Palik & Dumroese 2014). In Britain the restoration of native
63 woodland from plantations on ancient woodland sites has received increasing
64 attention (Pryor, Curtis & Peterken 2002; Thompson *et al.* 2003; Harmer &
65 Thompson 2013). Ancient woodland sites have had no other land use since at least
66 1600AD in England and Wales, or 1750AD in Scotland (Peterken 1977)). Native
67 forests on ancient woodland sites are important habitats for many rare and threatened
68 species (Peterken 1993), but between the 1930s and 1990s 40% of the remaining such
69 woodlands in Britain were converted to plantations, mostly of non-native conifers
70 (Spencer & Kirby 1992; Pryor & Smith 2002). Due to the increased recognition of the
71 value of native woodland it is now policy to restore these plantations (Harmer, Kerr &
72 Thompson 2010). Despite being greatly changed from native woodland, they often
73 retain features such as veteran trees, coppice stools and remnant ground flora (Pryor,
74 Curtis & Peterken 2002), making them good candidates for the successful restoration
75 of native forest.

76 Degraded forests can be restored through clearfelling of the existing canopy, or by
77 removing trees over an extended period of time (Stanturf, Palik & Dumroese 2014).
78 Whilst the effects of different conifer removal regimes on tree regeneration have been
79 investigated on plantations on ancient woodland sites (Harmer & Kiewitt 2006;

80 Harmer, Kiewitt and Morgan 2012), there has been little investigation into effects on
81 other taxa. As different restoration approaches cause disturbances of different
82 intensities and patterns they are likely to have a different impact on the ground flora
83 (Roberts & Gilliam 2014).

84 This study compares two restoration methods – clearfelling planted conifers versus
85 their gradual removal – and compares these to native woodland (as a reference
86 community) and to conifer plantations on ancient woodland sites not undergoing
87 restoration (the starting point of restoration). We focus on the effects of the restoration
88 methods on the ground flora and insect herbivore communities. Although the effects
89 of tree-removal practices on the ground flora community have begun to be explored,
90 they are still not well understood (Gilliam 2014). The plant diversity of forests is
91 largely determined by the ground flora (Gilliam 2007), and it is important to conserve
92 woodland ground flora species during restoration as many are slow to recolonize once
93 lost (Brunet & von Oheimb 1998; Hermy *et al.* 1999).

94

95 Restoration studies are often botanical in focus (Young 2000; Ruiz-Jaen & Aide
96 2005), and it is often assumed that successful restoration of the plant community leads
97 to the restoration of higher trophic levels. The diversity of herbivorous invertebrates is
98 indeed often correlated with the diversity of the plant community (Brown & Hyman
99 1986; Crisp, Dickinson & Gibbs 1998; Siemann, Haarstad & Tilman 1999; Rowe &
100 Holland 2013), and there is evidence to suggest that restoring the diversity and
101 structural complexity of vegetation will lead to the restoration of Hemipteran
102 assemblages in *Eucalyptus marginata* (Donn ex Sm.) forests (Moir *et al.* 2005).
103 However, other taxonomic groups and habitats need to be studied in order to
104 determine if this is a general effect or specific to certain taxa or habitats. Here we

105 investigate leaf-mining insects. These have not been widely used in restoration
106 ecology but, as a species-rich guild of specialist herbivores including species from
107 four insect orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera (Connor &
108 Taverner 1997)), they are a useful group for monitoring restoration. They are also
109 easy to collect and, as they live inside their food plant, host–plant relationships can be
110 accurately determined.

111

112 This study has three objectives: i) to determine whether the two restoration methods
113 differ in their impact on the plant species richness of the ground flora and woodland
114 specialist plants; ii) to assess whether plant species richness is correlated with leaf-
115 miner species richness and iii) to test whether the efficacy of the two restoration
116 approaches is affected by the type of woodland community being restored.

117 **Materials and methods**

118

119 **Field sites**

120 The study was carried out in the Forest of Dean, UK; a temperate forest spanning 106
121 km² in the West of England (51.789°N -2.546°W). The forest was previously
122 exploited for minerals and stone as well as timber, and contained areas managed as
123 coppice and wood pasture (Herbert 1996). The forest currently consists of a mix of
124 native broad-leaved and non-native conifer species.

125

126 Thirty-two plots were chosen, each 2 ha in size: eight plots managed as native broad-
127 leaved woodland (herein native plots), eight within conifer plantations not undergoing
128 restoration (herein plantations), eight within conifer plantations undergoing gradual
129 removal of planted trees for restoration (herein thinned plots), and eight within
130 clearfelled conifer plantations (herein clearfelled plots). All plots were on ancient
131 woodland sites. All plots were at least 15 m from the forest or clearfell edge. Plots
132 were spread across eight locations (blocks), with each block containing one plot under
133 each management regime.

134

135 The eight blocks consisted of two different forest types. Four of the blocks were on
136 acidic *Quercus* woodland (National Vegetation class W10 (*Quercus robur* - *Pteridium*
137 *aquilinum* - *Rubus fruticosus*) (Rodwell, 1991)) and four were on mesotrophic
138 *Fraxinus* woodland (National Vegetation class W8 (*Fraxinus excelsior* - *Acer*
139 *campestre* - *Mercurialis perennis*) (Rodwell, 1991)). Both these woodlands are
140 widespread in lowland Britain. For plantations, thinned plots, and clearfelled plots the
141 forest type refers to woodland that existed before conifer planting occurred. There

142 was evidence of deer presence, an important factor in determining the plant species
143 composition of forests (Waller 2014), in all plots.

144

145 On thinned plots, conifers are thinned every five years with thinning concentrated
146 around native broad-leaves. Plantations are also thinned every five years, with the
147 pattern of thinning determined to maximize conifer growth. In the clearfelled plots all
148 conifers were felled, and on all but one of these plots native broad-leaves were
149 planted. Native plots are thinned at most every ten years depending on the degree of
150 crown competition. Restoration commenced on thinned plots between seven and four
151 years prior to this study. Clearfelled plots were felled between four and ten years prior
152 to this study. Where possible, plantations, thinned plots, and clearfelled plots in the
153 same block had been planted with the same tree species. Plantations, thinned plots,
154 and clearfelled plots were planted between 1958 and 1976, and in the same block
155 were planted at most eight years apart (see Table S1 in Supporting Information for
156 further plot information).

157

158 **Plant sampling and classification**

159 Plots were sampled for plants every four weeks between late April 2011 and July
160 2011, with each of the 32 plots being sampled three times. Plots within the same
161 block were sampled on the same or consecutive days. During each sampling round a
162 100 m × 2 m transect, or on plots narrower than 100 m (due to the forest shape)
163 multiple transects with a combined area of 200 m², were randomly placed in each
164 plot. A gap of 1 m was left between transects shorter than 100 m to prevent plants
165 being counted twice. All transects within a plot were parallel, and transects used for
166 different sampling rounds were at least 5 m apart.

167

168 Along each transect all vascular plants excluding Lycopodiopsida were identified.
169 Plants with a d.b.h. less than 5 cm, and shorter than 2 m, excluding the native trees
170 planted on clearfelled plots, were counted as ground flora and each species was
171 assigned a species cover score (Fehmi 2010) using the Domin scale; 1 = <4 % species
172 cover – very scarce, 2 = <4 % – scarce, 3 = <4 % – scattered, 4 = 4–10%, 5 = 11–
173 25%, 6 = 26–33%, 7 = 34–50%, 8 = 51–75%, 9 = 76–90%, 10 = 91–100% (Mueller-
174 Dombois & Ellenberg 1974). Domin scores were back-transformed to continuous
175 percentage cover values using the Domin 2.6 transformation (Currall 1987).
176 Following transformation the mean abundance of each species from the three
177 sampling rounds was calculated. These mean values were used in the statistical
178 analyses. Species in the ground flora were classed as woodland species if “broad
179 leaved, mixed and yew woodland” was identified by Hill, Preston and Roy (2004) as
180 one of their broad habitats in the British Isles.

181

182 **Leaf-miner sampling**

183 Plots were sampled for leaf-miners between late April 2011 and August 2011. Each of
184 the 32 plots was sampled four times. Plots within the same block were sampled on the
185 same or consecutive days. The same transects were used as for plant surveys, with an
186 additional round of sampling, following the same transect methodology, in August
187 2011. Along each transect all leaves up to 2 m above the ground were inspected for
188 leaf-mines and all leaves with mines collected.

189

190 Leaf-miners were reared in the laboratory. The combination of leaf-mine morphology,
191 host plant species and adult miner morphology were used to identify leaf-miners using
192 the British Leafminers website (2015) and Pitkin *et al.* (2015).

193

194 **Statistical analyses**

195

196 **Objective 1: Do the two restoration methods differ in their impact on the ground**

197 **flora?** The effects of restoration method on the total ground flora and woodland

198 species ground flora were analysed using generalized linear mixed effects models.

199 Management regime (native, plantation, thinned or clearfelled), forest type (acidic

200 *Quercus* or mesotrophic *Fraxinus*), and their interaction were modelled as fixed

201 factors to analyse their effects on total ground flora species richness and woodland

202 species ground flora richness of plots. Block was added as a random effect to all

203 models to account for the blocked design of this study.

204

205 To evaluate the similarity in species composition of ground flora and woodland

206 species ground flora between management regimes the Bray-Curtis dissimilarity was

207 used. Non-metric multidimensional scaling (NMDS) was used for visual inspection of

208 the similarities between plots. The effects of management regime, and of the

209 interaction between management regime and forest type on the community

210 composition of ground flora and woodland species ground flora were analysed using

211 permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001)

212 with 9999 permutations. Data were permuted within blocks to account for the nesting

213 of plots within blocks. Significant differences may be due to different within-group

214 variation or different mean values (Warton, Wright & Wang 2012). Therefore, prior

215 to all PERMANOVA analyses a test for homogeneity of multivariate dispersion was
216 performed using 9999 permutations (Anderson 2006). For all such tests no difference
217 in multivariate dispersion was found between plots of different types, and we are
218 confident that significant results from PERMANOVA reflect differences in mean
219 values.

220

221 Due to the split-plot design of this study, with management regime assigned to plots
222 within blocks and forest type assigned to whole blocks, the main effect of forest type
223 could not be analysed. It uses a different error term from the main effect of
224 management regime and the forest type–management regime interaction (Snedecor &
225 Cochran 1989), and the software used to perform PERMANOVA did not allow the
226 use of two different error terms.

227

228 **Objective 2: Is plant species richness correlated with leaf-miner species richness?**

229 Rarefied leaf-miner species richness was calculated for each plot to adjust for
230 differences in abundance (Gotelli & Colwell 2001). This estimated the expected
231 species richness if 10 leaf-mines were sampled in each plot; the smallest number of
232 mines found in a plot with the exception of one plot where no mines were found.
233 Estimates made using a rarefied sample size of 50 individuals were comparable,
234 but led to plots being excluded due to having <50 mines. A rarefied sample size
235 of 10 was therefore preferred to maximize the plot sample size.

236

237 Rarefied richness was analysed using a general linear mixed effects model. The plant
238 species richness of plots, as well as management regime, forest type, and all two-way

239 interactions between these were modelled as fixed factors. Block was added as a
240 random effect to all models to account for the blocked design of this study.

241

242 **Objective 3: Is the efficacy of the two restoration approaches affected by forest**
243 **type?**

244 Forest type was included in the models described above. Although the effect of forest
245 type on ground flora species composition could not be statistically assessed using our
246 statistical models, PERMANOVA was able to determine if forest type interacted with
247 management regime to affect species composition. The main effect of forest type on
248 ground flora composition was determined graphically using NMDS.

249

250 **Model simplification and statistical software**

251 Maximum models were simplified using likelihood ratio tests (Bolker 2008).
252 Explanatory variables were retained in models, and considered significant, if their
253 removal resulted in a significant change in model deviance. The validity of final
254 models was checked using visual examination of residuals (Bolker *et al.* 2009). *Post*
255 *hoc* Tukey tests were performed for all pairwise comparisons of fixed factors, and
256 interactions between fixed factors, retained in optimal models, with *P* values adjusted
257 using the false discovery rate method (Benjamini & Hochberg 1995; Verhoeven,
258 Simonsen & McIntyre 2005; Pike 2011). If plant species richness, or an interaction
259 between plant species richness and another variable, was retained in the optimal
260 model of leaf-miner richness this was analysed graphically using effect displays (Fox,
261 2003). These show the predicted relationship between main effects and their
262 interactions on the response variable, as modelled using linear models such as those
263 performed here. Generalized linear mixed effect models used the Poisson distribution

264 and log link function (Bolker *et al.* 2009), and all linear models were fitted by
265 maximum likelihood estimates.

266

267 All analyses were conducted in R (R Core Team 2012). Package ‘lme4’ (Bates,
268 Maechler & Bolker 2012) was used to fit mixed models. Tukey tests were carried out
269 in the ‘multcomp’ package (Hothorn, Bretz & Westfall 2008). Effect displays were
270 produced using the ‘effects’ package (Fox 2003). Package ‘vegan’ (Oksanen *et al.*
271 2012) was used for NMDS plots, tests for homogeneity of multivariate dispersion,
272 PERMANOVA, and rarefaction.

273 **Results**

274

275 **Objective 1: Do the two restoration methods differ in their impact on the ground**

276 **flora?** One hundred and seventy-nine ground flora species were identified in the 32
277 plots, 167 to species level and 12 to genus, comprising 110 genera in 53 families (see
278 Table S2). Of these 86 were woodland species, comprising 69 genera in 47 families.
279 Management regime had a significant effect on species richness (Likelihood ratio test:
280 $\chi^2 = 65.35$, d.f.= 3, $P < 0.001$) and clearfelled plots had significantly more ground flora
281 species overall than other plots (Fig. 1a). However, all plots contained woodland
282 species and there was no significant effect of management regime on woodland
283 species richness (Likelihood ratio test; $\chi^2 = 1.83$, d.f.= 3, $P = 0.607$, Fig. 1b).

284

285 The overall ground flora community composition differed significantly between
286 management regimes (Pseudo $F = 4.05$, d.f. = 3, $P < 0.001$). Plantations and thinned
287 plots had a similar community composition intermediate between that of native and
288 clearfelled plots (Fig. 2a). The woodland species subset of the ground flora
289 community showed a different pattern from that of the ground flora in general.
290 Woodland species composition differed between management regimes (Pseudo $F =$
291 4.08 , d.f.=3, $P < 0.001$) but thinned, plantations and clearfelled plots overlapped in
292 their composition whilst native plots had a different woodland species composition
293 (Fig. 2b).

294

295 **Objective 2: Is plant species richness correlated with leaf-miner species richness?**

296 In total 10 025 mines were collected. Of these 9771 could be identified to at least
297 order level and comprised 122 species (see Table S3): 68 Lepidoptera species and

298 four Lepidoptera taxa identified to genus level, 38 Diptera species and two Diptera
299 taxa identified to genus level, 11 Hymenoptera species and one Hymenoptera taxon
300 identified to order level, and two Coleoptera species.

301

302 The relationship between plant and rarefied herbivore species richness was not
303 consistent between the different management regimes. Thus, there was a significant
304 interaction between plant species richness and management regime (Likelihood ratio
305 test: $\chi^2 = 15.20$, d.f.= 3, $P = 0.002$). On plantations, thinned and native plots, there
306 was a positive relationship between leaf-miner species richness and plant species
307 richness (Figs. 3a, 3b, 3c). However, on clearfelled plots there was a negative
308 relationship between leaf-miner species richness and plant species richness (Fig. 3d).

309

310 **Objective 3: Is the efficacy of the two restoration approaches affected by forest**
311 **type?**

312 There was a significant effect of forest type on both total ground flora species richness
313 (Likelihood ratio test: $\chi^2 = 5.61$, d.f.= 1, $P = 0.018$) and woodland species richness
314 (Likelihood ratio test; $\chi^2 = 7.69$, d.f.= 1, $P = 0.006$) with mesotrophic *Fraxinus* plots
315 having a greater mean species richness than acidic *Quercus* plots in both cases (Total
316 ground flora species; 49.36 ± 8.5 vs. 32.19 ± 5.85 ; Woodland species; 23.56 ± 1.83
317 vs. 13.75 ± 2.79). Plots on the two different forest types also differed in total ground
318 flora species composition (Fig. 2a) and woodland species composition (Fig. 2b).

319

320 However, there was no interaction between management regime and forest type
321 affecting either total ground flora community composition (Pseudo $F = 1.33$, d.f. = 3,
322 $P = 0.110$), total ground flora species richness (Likelihood ratio test: $\chi^2 = 4.46$, d.f.=

323 3, $P = 0.216$), woodland species composition (Pseudo $F = 1.28$, d.f. = 3, $P = 0.173$),
324 or woodland species richness (Likelihood ratio test; $\chi^2 = 1.83$, d.f.= 3, $P = 0.605$).
325 Neither was there an effect of forest type on leaf-miner species richness (Likelihood
326 ratio test: $\chi^2 = 0.69$, d.f.= 1, $P = 0.407$). Thus the two restoration approaches have the
327 same impact on each type of woodland.

328

329 **Discussion**

330 During restoration it is important not only to re-establish, but to also maintain any
331 species native to the target habitat already present. Both of the restoration methods
332 studied here maintained woodland ground flora species. However, the restoration
333 methods differed in their effects in other ways. Clearfelled plots had greater ground
334 flora species richness than thinned plots, and leaf-miner species richness increased
335 with plant species richness on thinned plots but not on clearfelled plots. Forest type
336 did not interact with the restoration method, demonstrating that the two approaches
337 have a consistent effect on different plant communities.

338

339 There are two caveats to consider when interpreting these results. First, plant
340 community data from plots prior to clearfelling or the onset of thinning were not
341 available. Therefore, any differences seen between plots cannot be conclusively
342 attributed to their management. However, there is no reason to suspect that the plant
343 communities under the different management regimes differed systematically prior to
344 restoration. Secondly, logistical constraints meant that leaf-miners were only sampled
345 from vegetation up to 2-m tall, i.e. the tree canopy was not sampled. However,
346 clearfelled plots had few trees taller than 2 m, and the canopy of plantations and
347 thinned plots mainly consisted of conifers. Although conifers do host leaf-miners no

348 mines were found on conifer leaves during this study. We are therefore confident that
349 the samples from plantations, clearfelled and thinned plots reflect their leaf-miner
350 community. The native plots, however, had an extensive canopy cover of broad-
351 leaved trees and their species richness of leaf-miners may be higher than reported
352 here.

353

354 **The effect of restoration method on ground flora**

355 The potential of plantations on ancient woodland sites to be restored to native
356 woodland was confirmed by the presence of many woodland species, such as *Arum*
357 *maculatum* (L.), *Mercurialis perennis* (L.), and *Anemone nemorosa* (L.) in their
358 ground flora. Indeed plantations had the same number of woodland species in their
359 ground flora as native plots. Furthermore, neither approach to removing conifers
360 resulted in a decline in woodland ground flora species as restoration plots had the
361 same number, and a similar composition, of woodland ground flora species as
362 unrestored plantations. Due to the slow migration of many woodland plants (Brunet &
363 von Oheimb 1998; Hermy *et al.* 1999) maintaining their populations is an important
364 requirement of plantation restoration, and both approaches to restoration achieved
365 this.

366

367 The thinning regime studied here differs little from the management regime on
368 plantations not undergoing restoration, and both regimes result in a similar level of
369 disturbance. This explains the similarity in woodland species composition and
370 richness on these plots. Clearfelling of forests often results in the decline and loss of
371 woodland species (Hannerz & Hånell 1997; Roberts & Zhu 2002; Godefroid,
372 Rucquoi & Koedam 2005), here though clearfelled plots had the same number of

373 woodland species as the other management regimes. There are four mechanisms
374 whereby ground flora species may reappear on sites following disturbance such as
375 that caused by clearfelling; survival *in situ*, vegetative regeneration, regeneration from
376 the seed bank, and regeneration from dispersed propagules (Roberts and Gilliam
377 2014). Due to the absence of pre-restoration species lists we cannot be certain if these
378 woodland species were present in the community before felling, or if they have
379 subsequently colonized or regenerated from the seed bank of the clearfelled plots.
380 However, they are unlikely to have all germinated from the seed bank, as, with the
381 exception of *Rubus fruticosus* (L. agg.), woodland species do not produce long-lived
382 seed banks (Thompson, Bakker & Bekker 1997). Furthermore, many woodland
383 species have poor dispersal capabilities (Brunet & von Oheimb 1998; Hermy *et al.*
384 1999; Verheyen *et al.* 2003). However, *Deschampsia cespitosa* (L.) P. Beauv., and *A.*
385 *nemorosa*, both dispersal-limited woodland species (Verheyen & Hermy 2001), were
386 found on plantations as well as clearfelled plots. It is therefore most likely that
387 survival *in situ* and vegetative regeneration from surviving vegetation are the
388 mechanisms responsible for the appearance of woodland species in the ground flora of
389 clearfelled plots, suggesting that remnant woodland species populations can survive
390 clearfelling at least for the four to ten year post-felling window during which this
391 study was conducted. Many woodland species take advantage of canopy gaps and soil
392 disturbance (Brunet, Falkengren-Grerup & Tyler 1996; Brunet, Falkengren-Grerup &
393 Tyler 1997), and removal of the canopy can increase flowering, seed production, or
394 the vegetative spread of some woodland species (Hughes & Fahey 1991; Mayer, Abs
395 & Fischer 2004), aiding their survival following clearfelling. Furthermore, the
396 abundant *Pteridium aquilinum* (L.) Kuhn cover on the clearfelled plots may have
397 allowed shade-tolerant woodland plants to survive (Pakeman & Marrs 1992).

398

399 Clearfelled plots had the greatest overall ground flora species richness. Canopy
400 opening of abandoned coppice also results in an increase in species richness (Vild *et*
401 *al.* 2013), and the species richness of clearfelled plots may reflect the community
402 present following historical coppicing or clearfelling for timber. Clearfelling results in
403 soil disturbance, more light reaching the ground (Ash & Barkham 1976; Collins &
404 Pickett 1988; Mitchell 1992) and an increased availability of colonization sites,
405 leading to an increase in species richness through the dispersal of propagules into
406 clearfelled plots and/or regeneration from the seed bank (Roberts & Zhu 2002; Pykälä
407 2004). This is reflected in the species composition of clearfelled plots, which
408 contained many ruderal and grassland species such as *Chamerion angustifolium* (L.),
409 *Buddleja davidii* (Franch.) and *Ranunculus acris* (L.).

410

411 The woodland species composition of plantations, clearfelled or thinned plots did not
412 resemble the native plots. This is likely due to the age of native plots; they have
413 existed as native woodland for decades, or centuries, enabling the establishment of
414 slow colonizing woodland species. There is no list of ancient woodland indicator
415 species for the Forest of Dean, but species such as *A. nemorosa*, *M. perennis*, and *Ilex*
416 *aquifolium* (L.), have been identified as ancient woodland species in other regions
417 (Hermy *et al.* 1999; Rose & O'Reilly 2006). While these species were present in
418 plantations, thinned plots, and clearfelled plots, they were more abundant in the native
419 plots. Continued monitoring is required to see if the woodland species composition of
420 clearfelled and thinned plots moves towards that of native plots.

421

422 **The relationship between plant species richness and leaf-miner species richness**

423 The diversity of phytophagous invertebrates often follows that of the plant community
424 (Brown & Hyman 1986; Crisp, Dickinson & Gibbs 1998; Siemann, Haarstad &
425 Tilman 1999; Rowe & Holland 2013), and leaf-miner species richness did increase
426 with plant species richness on plantations, thinned and native plots. Most leaf-miners
427 are specialists on a small number of related host plants (Memmott, Godfray & Gauld
428 1994). Therefore, as plant species richness increases more niches are available for
429 leaf-miner species, and more leaf-miner species are able to establish in the
430 community. However, greater plant species richness did not necessarily lead to
431 greater species richness of leaf-miners. On clearfelled plots leaf-miner species
432 richness did not increase as plant species richness increased, demonstrating that the
433 relationship between plant species richness and invertebrate herbivore species
434 richness can differ under different management regimes.

435

436 Although not measured here, clearfelled plots had greater, denser, vegetation cover
437 than the other plots. The vegetation cover on clearfelled plots may make it difficult
438 for leaf-miners to locate host plants in species rich communities using visual or
439 chemical cues (McNair, Gries & Gries 2000; Jactel *et al.* 2011; Dulaurent *et al.* 2012),
440 preventing them from establishing. This could occur through reduced resource
441 concentration, whereby herbivores are less able to find host plants when they do not
442 form dense stands (Root 1973), and/or reduced focal plant apparency, whereby
443 herbivores are less able to find host plants when they are concealed by taller non-host
444 plants (Floater & Zalucki 2000; Hughes 2012; Castagneyrol *et al.* 2013). When plant
445 species richness is lower, but the vegetation cover is high, these mechanisms will not
446 occur, and leaf-miners may be even more likely to establish due to the ease of locating

447 host plants when they form dense stands. Further investigation is needed to determine
448 if these mechanisms explain our results.

449

450 **The effect of forest type on restoration outcome**

451 Forest type had no effect on leaf-miner species richness, but did affect the species
452 richness of the ground flora and richness of woodland species in the ground flora,
453 with mesotrophic *Fraxinus* plots having a greater species richness of both these
454 groups. However, there were no significant interactions between forest type and
455 management regime. Differences between the forest types are differences in the
456 number of species present and not in the patterns of species richness between
457 management regimes. This is important as it means that, for these two forest types at
458 least, the results from a study of the ground flora community on one forest type can be
459 applied to the other, saving time and money.

460

461 **Conclusions**

462 Both restoration methods conserved the woodland plant species richness of sites
463 during restoration. This has important management implications. Which restoration
464 method to use depends on many factors, but the results here suggest that both can be
465 considered. For example, clearfelling may be the only option possible on sites
466 that cannot easily be visited multiple times for thinning, and these results
467 suggest that this will not be at the expense of the woodland ground flora.
468 However, we found that the method of restoration influenced the relationship between
469 plant and leaf-miner species richness. If high invertebrate species richness is an aim of
470 restoration the gradual thinning approach to restoration is better, as leaf-miner species
471 richness did not increase with plant species richness on clearfelled plots. This also

472 demonstrates that species higher up the food chain, such as herbivores, should be
473 monitored during restoration. Restoration aims to restore the integrity of degraded
474 systems, and this necessarily involves observing more than just plants.
475

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478 the Forestry Commission. We thank Emily Aldridge for assisting with data collection
479 and Ralph Harmer for his comments.

480

481 **Data accessibility**

482 Plot information uploaded as online supporting information.

483 Plant and leaf-miner species richness, and plant and leaf-miner species found on each

484 site: DRYAD entry doi:10.5061/dryad.q20jf

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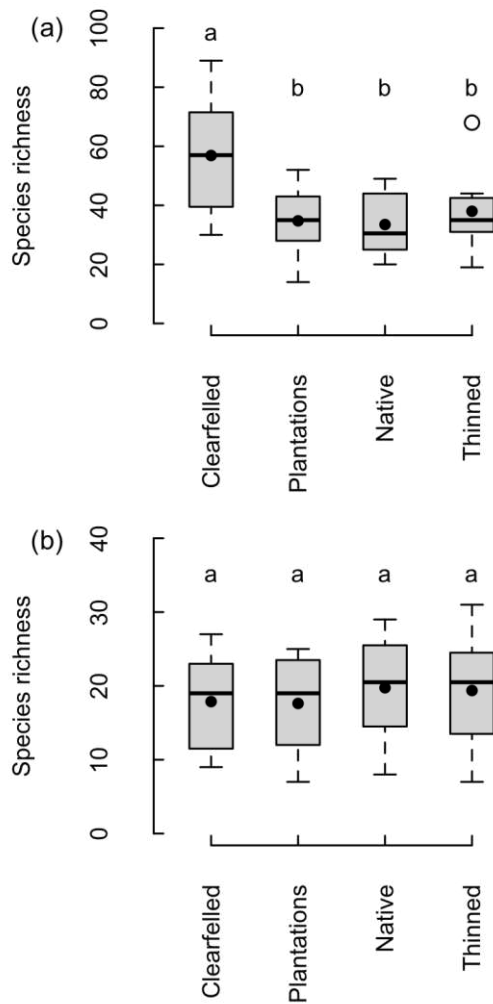
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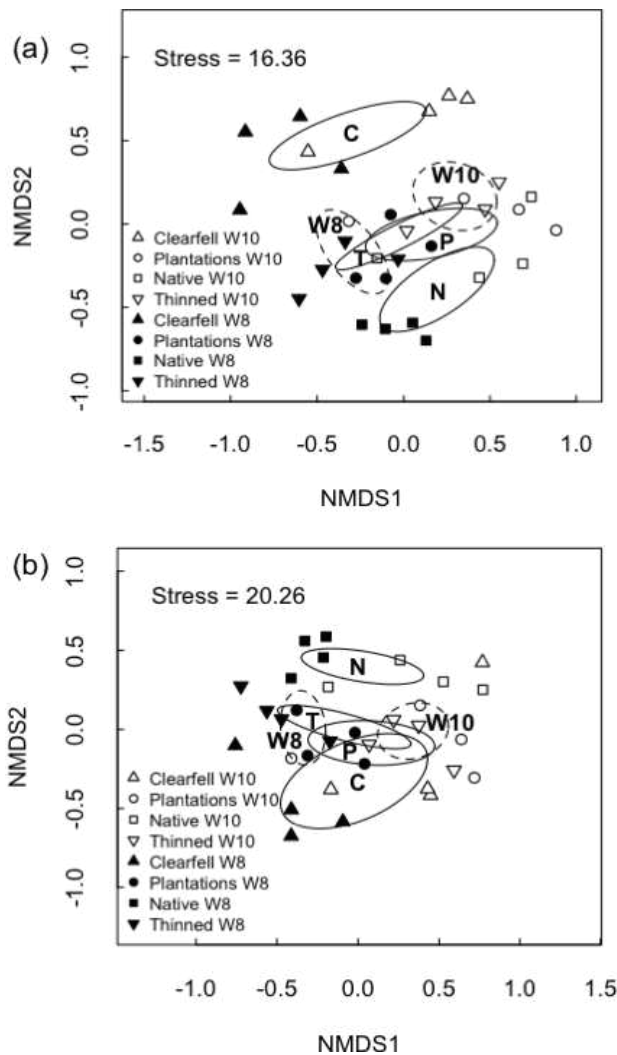
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698

699 **Figure 1.** Plant species richness of plots under the different management regimes: a)
 700 the total ground flora species richness; b) the woodland ground flora species richness.
 701 Different letters within each panel indicate a significant difference ($P < 0.0001$).



702

703 **Figure 2.** Non-metric multidimensional scaling (NMDS) plot of the composition of

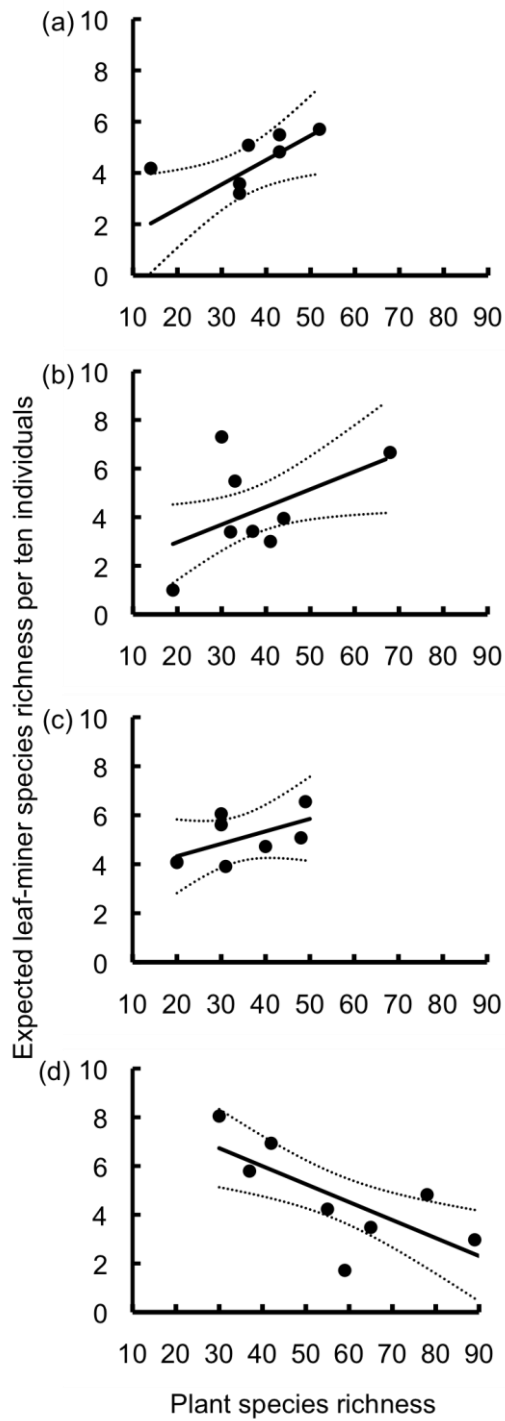
704 the ground flora (a), and the woodland species in the ground flora (b). Each point

705 represents a plot. Ellipses represent 95% confidence intervals of the mean score of

706 management regimes (solid lines) and mean score of forest types (dashed lines).

707 Clearfell = C, Plantations = P, Native = N, Thinned = T. Acidic *Quercus* woodland =

708 W10, mesotrophic *Fraxinus* woodland = W8.



709

710 **Figure 3.** The relationship between plant species richness and rarefied leaf-miner
 711 species richness for: (a) plantations, (b) thinned plots, (c) native plots, and (d)
 712 clearfelled plots. Dashed lines indicate 95% confidence intervals. The underlying
 713 model is a general linear mixed model with site as a random effect.

714 **Supporting Information**

715 Additional supporting information may be found in the online version of this article:

716 **Table S1.** Details of the study plots used in this study.

717 **Table S2.** Plant species found in the ground flora of study plots.

718 **Table S3.** Leaf-miner species found in study plots.