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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

4   **Atkinson, B[1]*, Bailey, S[2] , Vaughan I.P.[3] & Memmott, J[1]**

5   [1] School of Biological Sciences, University of Bristol, Life Sciences Building, 24

6   Tyndall Avenue, Bristol, BS8 1TQ, UK

7   [2]Forestry Commission, Silvan House, 231 Corstorphine Road, Edinburgh, EH12 7AT,

8   UK

9   [3]Cardiff School of Biosciences, Cardiff University, Museum Avenue, Cardiff CF10

10   3AX, UK

11   *** Corresponding author:** beth.atkinson86@gmail.com

12

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14

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Summary

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

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

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

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

50

51   **5.** Forest type did not affect the response to restoration method, i.e. there was no

52   interaction between management regime and forest type for any of the variables

53   measured.

54

55   **6.** *Synthesis and applications.* Both the clearfelling and gradual thinning approaches

56   to plantation restoration maintained the woodland species in the ground flora of

57   plantations. However, these restoration methods differed in their effects on the leaf-

58   miner – plant species richness relationship. It is often assumed that during restoration

59   increases in plant-species richness lead to increases invertebrate herbivore richness,

60   but this was not the case on clearfelled sites. This study demonstrates the importance

61   of testing and comparing restoration methods, and monitoring invertebrates as well as

62   plants during restoration.

63

Introduction

68 Ecological restoration is essential for creating resilient ecological networks, ensuring

69 sustainable provision of ecosystem services, and conserving threatened species and

70 habitats (Young 2000; Hobbs & Harris 2001; Lawton *et al*. 2010). The restoration of

71 degraded forests is taking place across the globe, and although forests vary in

72 structure and species composition, similar methods are used for forest restoration

73 worldwide (Stanturf, Palik & Dumroese 2014). In Britain the restoration of native

74 woodland from plantations on ancient woodland sites has received increasing

75 attention (Pryor, Curtis & Peterken 2002; Thompson *et al.* 2003; Harmer &

76 Thompson 2013). Ancient woodland sites have had no other land use since at

77 least1600AD in England and Wales, or 1750AD in Scotland (Peterken 1977)). Native

78 forests on ancient woodland sites are important habitats for many rare and threatened

79 species (Peterken 1993), but between the 1930's and 1990's 40% of the remaining

80 such woodlands in Britain were converted to plantations, mostly of non-native

81 conifers (Spencer & Kirby 1992; Pryor & Smith 2002). Due to the increased

82 recognition of the value of native woodland it is now policy to restore these

83 plantations (Harmer, Kerr & Thompson 2010). Despite being greatly changed from

84 native woodland, they often retain features such as veteran trees, coppice stools and

85 remnant ground flora (Pryor, Curtis & Peterken 2002), making them good candidates

86 for the successful restoration of native forest.

87 Degraded forests can be restored through clearfelling of the existing canopy, or by

88 removing trees over an extended period of time (Stanturf, Palik & Dumroese 2014).

89 Whilst the effects of different conifer removal regimes on tree regeneration have been

90 investigated on plantations on ancient woodland sites (Harmer & Kiewitt 2006;

91   Harmer, Kiewitt and Morgan 2012), there has been little investigation into effects on

92   other taxa. As different restoration approaches cause disturbances of different

93   intensities and patterns they are likely to have a different impact on the ground flora

94   (Roberts & Gillliam 2014).

95   This study compares two restoration methods – clearfelling planted conifers versus

96   their gradual removal – and compares these to native woodland (as a reference

97   community) and to conifer plantations on ancient woodland sites not undergoing

98   restoration (the starting point of restoration). We focus on the effects on the ground

99   flora and insect herbivore communities. Although the effects of tree-removal practises

100   on the ground flora community have begun to be explored, they are still not well

101   understood (Gilliam 2014). The plant diversity of forests is largely determined by the

102   ground flora (Gilliam 2007), and it is important to conserve woodland ground flora

103   species during restoration as many are slow to re-colonise once lost (Brunet & von

104   Oheimb 1998; Hermy et al. 1999).

105

106   Restoration studies are often botanical in focus (Young 2000; Ruiz-Jaen & Aide

107   2005), and it is often assumed that successful restoration of the plant community leads

108   to the restoration of higher trophic levels. The diversity of herbivorous invertebrates is

109   indeed often correlated with the diversity of the plant community (Brown & Hyman

110   1986; Crisp, Dickinson & Gibbs 1998; Siemann, Haarstad & Tilman 1999; Rowe &

111   Holland 2013), and there is evidence to suggest that restoring the diversity and

112   structural complexity of vegetation will lead to the restoration of Hemipteran

113   assemblages in *Eucalyptus marginata* (Donn ex Sm.) forests (Moir *et al.* 2005).

114   However, other taxonomic groups and habitats need to be studied in order to

115   determine if this is a general effect or specific to certain taxa or habitats. Here we

116   investigate leaf-mining insects. These have not been widely used in restoration

117   ecology but, as a species rich guild of specialist herbivores including species from

118   four insect orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera (Connor &

119   Taverner 1997)), they are a useful group for monitoring restoration. They are also

120   easy to collect and, as they live inside their food plant, host-plant relationships can be

121   accurately determined.

122

123   This study has three objectives: 1) To determine whether the two restoration methods

124   differ in their impact on the plant species richness of the ground flora and woodland

125   specialist plants; 2) To assess whether plant species richness is correlated with leaf-

126   miner species richness; 3) To test whether the efficacy of the two restoration

127   approaches is affected by the type of woodland community being restored.

Materials and methods

Field sites

The study was carried out in the Forest of Dean, UK; a temperate forest spanning 106 km^2 in the West of England (51.789 N, -2.546 W). The forest was previously exploited for minerals and stone as well as timber, and contained areas managed as coppice and wood pasture (Herbert 1996). The forest currently consists of a mix of native broad-leaved and non-native conifer species.

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

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

153   was evidence of deer presence, an important factor in determining the plant species

154   composition of forests (Waller 2014), in all plots.

155

156   On thinned plots, conifers are thinned every 5 years with thinning concentrated

157   around native broadleaves. Plantations are also thinned every 5 years, with the pattern

158   of thinning determined to maximise conifer growth. In the clearfelled plots all

159   conifers were felled, and on all but one of these plots native broadleaves were planted.

160   Native plots are thinned at most every 10 years depending on the degree of crown

161   competition. Restoration commenced on thinned plots between 7 and 4 years prior to

162   this study. Clearfelled plots were felled between 4 and 10 years prior to this study.

163   Where possible plantations, thinned plots, and clearfelled plots in the same block had

164   been planted with the same tree species. Plantations, thinned plots, and clearfelled

165   plots were planted between 1958 and 1976, and in the same block were planted at

166   most eight years apart (see Table S1 in Supporting Information for further plot

167   information).

168

169   **Plant sampling and classification**

170   Plots were sampled for plants every four weeks between late April 2011 and July

171   2011, with each of the 32 plots being sampled three times. Plots within the same

172   block were sampled on the same or consecutive days. During each sampling round a

173   100 m x 2 m transect, or on plots narrower than 100 m (due to the forest shape)

174   multiple transects with a combined area of 200 m^2, were randomly placed in each

175   plot. A gap of 1 m was left between transects shorter than 100 m to prevent plants

176   being counted twice. All transects within a plot were parallel, and transects used for

177   different sampling rounds were at least 5 m apart.

178

179   Along each transect all vascular plants excluding Lycopodiopsida were identified.

180   Plants with a diameter at breast height less than 5 cm, and shorter than 2 m, excluding

181   the native trees planted on clearfelled plots, were counted as ground flora and each

182   species was assigned a species cover score (Fehmi 2010) using the Domin scale; 1 =

183   <4 % species cover - very scarce, 2 = <4 % - scarce, 3 = <4 % - scattered, 4 = 4–10%,

184   5 = 11–25%, 6 = 26–33%, 7 = 34–50%, 8 = 51–75%, 9 = 76–90%, 10 = 91–100%

185   (Mueller-Dombois & Ellenberg 1974). Domin scores were back-transformed to

186   continuous percentage cover values using the Domin 2.6 transformation (Currall

187   1987). Following transformation the mean abundance of each species from the three

188   sampling rounds was calculated. These mean values were used in the statistical

189   analyses. Species in the ground flora were classed as woodland species if "broad

190   leaved, mixed and yew woodland" was identified by Hill, Preston and Roy (2004) as

191   one of their broad habitats in the British Isles.

192

193   **Leaf-miner sampling**

194   Plots were sampled for leaf-miners between late April 2011 and August 2011. Each of

195   the 32 plots was sampled four times. Plots within the same block were sampled on the

196   same or consecutive days. The same transects were used as for plant surveys, with an

197   additional round of sampling, following the same transect methodology, in August

198   2011. Along each transect all leaves up to 2 m above the ground were inspected for

199   leaf-mines and all leaves with mines collected.

200

201   Leaf-miners were reared in the laboratory. The combination of leaf-mine morphology,

202   host plant species and adult miner morphology was used to identify leaf-miners using

203   the British Leafminers website (n.d.) and Pitkin *et al.* (n.d.).

204

205   **Statistical analyses**

206

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

208   **flora?** The effect of restoration method on the total ground flora and woodland

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

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

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

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

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

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

215

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

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

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

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

220   between management regime and forest type on the community composition of

221   ground flora and woodland species ground flora were analysed using permutational

222   multivariate analysis of variance (PERMANOVA) (Anderson 2001) with 9999

223   permutations. Data were permuted within blocks to account for the nesting of plots

224   within blocks. Significant differences may be due to different within-group variation

225   or different mean values (Warton, Wright & Wang 2012). Therefore, prior to all

226 PERMANOVA analyses a test for homogeneity of multivariate dispersion was

227 performed using 9999 permutations (Anderson 2006). For all such tests no difference

228 in multivariate dispersion was found between plots of different types, and we are

229 confident that significant results from PERMANOVA reflect differences in mean

230 values.

231

232 Due to the split-plot design of this study, with management regime assigned to plots

233 within blocks and forest type assigned to whole blocks, the main effect of forest type

234 could not be analysed. It uses a different error term from the main effect of

235 management regime and the forest type - management regime interaction (Snedecor

236 & Cochran 1989), and the software used to perform PERMANOVA did not allow the

237 use of two different error terms.

238

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

240 Rarefied leaf-miner species richness was calculated for each plot to adjust for

241 differences in abundance (Gotelli & Colwell 2001). This estimated the expected

242 species richness if 10 leaf-mines were sampled in each plot; the smallest number of

243 mines found in a plot with the exception of one plot where no mines were found.

244 Estimates made using a rarefied sample size of 50 individuals were comparable,

245 but led to plots being excluded due to having <50 mines. A rarefied sample size

246 of 10 was therefore preferred to maximise the plot sample size.

247

248 Rarefied richness was analysed using a general linear mixed effects model. The plant

249 species richness of plots, as well as management regime, forest type, and all two-way

250   interactions between these were modelled as fixed factors. Block was added as a

251   random effect to all models to account for the blocked design of this study.

252

253   **Objective 3: Is the efficacy of the two restoration approaches affected by forest**

254   **type?**

255   Forest type was included in the models described above. Although the effect of forest

256   type on ground flora species composition could not be statistically assessed using our

257   statistical models, PERMANOVA was able to determine if forest type interacted with

258   management regime to affect species composition. The main effect of forest type on

259   ground flora composition was determined graphically using NMDS.

260

261   **Model simplification and statistical software**

262   Maximum models were simplified using likelihood ratio tests (Bolker 2008).

263   Explanatory variables were retained in models, and considered significant, if their

264   removal resulted in a significant change in model deviance. The validity of final

265   models was checked using visual examination of residuals (Bolker *et al.* 2009). *Post*

266   *hoc* Tukey tests were performed for all pair-wise comparisons of fixed factors, and

267   interactions between fixed factors, retained in optimal models, with *P* values adjusted

268   using the false discovery rate method (Benjamini & Hochberg 1995; Verhoeven,

269   Simonsen & McIntyre 2005; Pike 2011). If plant species richness, or an interaction

270   between plant species richness and another variable, was retained in the optimal

271   model of leaf-miner richness this was analysed graphically using effect displays (Fox,

272   2003). These show the predicted relationship between main effects and their

273   interactions on the response variable, as modelled using linear models such as those

274   performed here. Generalized linear mixed effect models used the Poisson distribution

275   and log link function (Bolker *et al.* 2009), and all linear models were fitted by

276   maximum likelihood estimates.

277

278   All analyses were conducted in R (R Core Team 2012). Package 'lme4' (Bates,

279   Maechler & Bolker 2012) was used to fit mixed models. Tukey tests were carried out

280   in the 'multcomp' package (Hothorn, Bretz & Westfall 2008). Effect displays were

281   produced using the 'effects' package (Fox 2003). Package 'vegan' (Oksanen *et al.*

282   2012) was used for NMDS plots, tests for homogeneity of multivariate dispersion,

283   PERMANOVA, and rarefaction.

284 **Results**

285

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

287 **flora?** One hundred and seventy-nine ground flora species were identified in the 32

288 plots, 167 to species level and 12 to genus, comprising 110 genera in 53 families (see

289 Table S2). Of these 86 were woodland species, comprising 69 genera in 47 families.

290 Management regime had a significant effect on species richness (Likelihood ratio test:

291 $\chi^2 = 65.35$, d.f.= 3, $P<0.001$) and clearfelled plots had significantly more ground flora

292 species overall than other plots (Fig. 1a). However, all plots contained woodland

293 species and there was no significant effect of management regime on woodland

294 species richness (Likelihood ratio test; $\chi^2 = 1.83$, d.f.= 3 , $P = 0.607$, Fig. 1b).

295

296 The overall ground flora community composition differed significantly between

297 management regimes (Pseudo $F = 4.05$, d.f. = 3, $P<0.001$). Plantations and thinned

298 plots had a similar community composition intermediate between that of native and

299 clearfelled plots (Fig. 2a). The woodland species subset of the ground flora

300 community showed a different pattern from that of the ground flora in general.

301 Woodland species composition differed between management regimes (Pseudo $F =$

302 4.08, d.f.=3, $P <0.001$) but thinned, plantations and clearfelled plots overlapped in

303 their composition whilst native plots had a different woodland species composition

304 (Fig. 2b).

305

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

307 In total 10,025 mines were collected. Of these 9771 could be identified to at least

308 order level and comprised 122 species (see Table S3): 68 Lepidoptera species and

309   four Lepidoptera taxa identified to genus level, 38 Diptera species and two Diptera

310   taxa identified to genus level, 11 Hymenoptera species and one Hymenoptera taxon

311   identified to order level, and two Coleoptera species.

312

313   The relationship between plant and rarefied herbivore species richness was not

314   consistent between the different management regimes. Thus, there was a significant

315   interaction between plant species richness and management regime (Likelihood ratio

316   test: $\chi^2 = 15.20$, d.f.= 3, $P = 0.002$). On plantations, thinned and native plots, there

317   was a positive relationship between leaf-miner species richness and plant species

318   richness (Figs. 3a, 3b, 3c). However, on clearfelled plots there was a negative

319   relationship between leaf-miner species richness and plant species richness (Fig. 3d).

320

321   **Objective 3: Is the efficacy of the two restoration approaches affected by forest**

322   **type?**

323   There was a significant effect of forest type on both total ground flora species richness

324   (Likelihood ratio test: $\chi^2 = 5.61$, d.f.= 1, $P = 0.018$) and woodland species richness

325   (Likelihood ratio test; $\chi^2 = 7.69$, d.f.= 1 , $P = 0.006$) with mesotrophic *Fraxinus* plots

326   having a greater mean species richness than acidic *Quercus* plots in both cases (Total

327   ground flora species; 49.36 ± 8.5 vs. 32.19 ± 5.85; Woodland species; 23.56 ± 1.83

328   vs.13.75 ± 2.79). Plots on the two different forest types also differed in total ground

329   flora species composition (Fig. 2a) and woodland species composition (Fig. 2b).

330

331   However, there was no interaction between management regime and forest type

332   affecting either total ground flora community composition (Pseudo $F = 1.33$, d.f. = 3,

333   $P = 0.110$), total ground flora species richness (Likelihood ratio test: $\chi^2 = 4.46$, d.f.=

334 3, $P = 0.216$), woodland species composition (Pseudo $F = 1.28$, d.f. $= 3$, $P = 0.173$),

335 or woodland species richness (Likelihood ratio test; $\chi^2 = 1.83$, d.f.$= 3$, $P = 0.605$).

336 Neither was there an effect of forest type on leaf-miner species richness (Likelihood

337 ratio test: $\chi^2 = 0.69$, d.f.$= 1$, $P = 0.407$). Thus the two restoration approaches have the

338 same impact on each type of woodland.

339

340 **Discussion**

341 During restoration it is important not only to re-establish, but to also maintain any

342 species native to the target habitat already present. Both of the restoration methods

343 studied here maintained woodland ground flora species. However, the restoration

344 methods differed in their effects in other ways. Clearfelled plots had greater ground

345 flora species richness than thinned plots, and leaf-miner species richness increased

346 with plant species richness on thinned plots but not on clearfelled plots. Forest type

347 did not interact with the restoration method, demonstrating that the two approaches

348 have a consistent effect on different plant communities.

349

350 There are two caveats to consider when interpreting these results. Firstly, plant

351 community data from plots prior to clearfelling or the onset of thinning were not

352 available. Therefore, any differences seen between plots cannot be conclusively

353 attributed to their management. However, there is no reason to suspect that the plant

354 communities under the different management regimes differed systematically prior to

355 restoration. Secondly, logistical constraints meant that leaf-miners were only sampled

356 from vegetation up to 2 m tall, i.e. the tree canopy was not sampled. However,

357 clearfelled plots had few trees taller than 2m, and the canopy of plantations and

358 thinned plots mainly consisted of conifers. Although conifers do host leaf-miners no

359   mines were found on conifer leaves during this study. We are therefore confident that

360   the samples from plantations, clearfelled and thinned plots reflect their leaf-miner

361   community. The native plots, however, had an extensive canopy cover of broadleaved

362   trees and their species richness of leaf-miners may be higher than reported here.

363

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

365   The potential of plantations on ancient woodland sites to be restored to native

366   woodland was confirmed by the presence of many woodland species, such as *Arum*

367   *maculatum* (L.), *Mercurialis perennis* (L.), and *Anemone nemorosa* (L.) in their

368   ground flora. Indeed plantations had the same number of woodland species in their

369   ground flora as native plots. Furthermore, neither approach to removing conifers

370   resulted in a decline in woodland ground flora species as restoration plots had the

371   same number, and a similar composition, of woodland ground flora species as

372   unrstored plantations. Due to the slow migration of many woodland plants (Brunet &

373   von Oheimb 1998; Hermy *et al.* 1999) maintaining their populations is an important

374   requirement of plantation restoration, and both approaches to restoration achieved

375   this.

376

377   The thinning regime studied here differs little from the management regime on

378   plantations not undergoing restoration, and both regimes result in a similar level of

379   disturbance. This explains the similarity in woodland species composition and

380   richness on these plots. Clearfelling of forests often results in the decline and loss of

381   woodland species (Hannerz & Hånell 1997; Roberts & Zhu 2002; Godefroid,

382   Rucquoij & Koedam 2005), here though clearfelled plots had the same number of

383   woodland species as the other management regimes. There are four mechanisms

384   whereby ground flora species may reappear on sites following disturbance such as

385   that caused by clearfelling; survival *in situ*, vegetative regeneration, regeneration from

386   the seed bank, and regeneration from dispersed propagules (Roberts and Gilliam

387   2014). Due to the absence of pre-restoration species lists we cannot be certain if these

388   woodland species were present in the community before felling, or if they have

389   subsequently colonised or regenerated from the seed bank of the clearfelled plots.

390   However, they are unlikely to have all germinated from the seed bank, as, with the

391   exception of *Rubus fruticosus* (L. agg.), woodland species do not produce long-lived

392   seed banks (Thompson, Bakker & Bekker 1997). Furthermore, many woodland

393   species have poor dispersal capabilities (Brunet & von Oheimb 1998; Hermy *et al.*

394   1999; Verheyen *et al*. 2003). However, *Deschampsia* cespitosa (L.) P. Beauv., and A.

395   *nemorosa*, both dispersal limited woodland species (Verheyen & Hermy 2001), were

396   found on plantations as well as clearfelled plots. It is therefore most likely that

397   survival *in situ* and vegetative regeneration from surviving vegetation are the

398   mechanisms responsible for the appearance of woodland species in the ground flora of

399   clearfelled plots, suggesting that remnant woodland species populations can survive

400   clearfelling at least for the four to 10 year post-felling window during which this

401   study was conducted. Many woodland species take advantage of canopy gaps and soil

402   disturbance (Brunet, Falkengren-Grerup & Tyler 1996; Brunet, Falkengren-Grerup &

403   Tyler 1997), and removal of the canopy can increase flowering, seed production, or

404   the vegetative spread of some woodland species (Hughes & Fahey 1991; Mayer, Abs

405   & Fischer 2004), aiding their survival following clearfelling. Furthermore, the

406   abundant *Pteridium aquilinum* (L.) Kuhn cover on the clearfelled plots may have

407   allowed shade tolerant woodland plants to survive (Pakeman & Marrs 1992).

408

409   Clearfelled plots had the greatest overall ground flora species richness. Canopy

410   opening of abandoned coppice also results in an increase in species richness (Vild *et*

411   *al.* 2013), and the species richness of clearfelled plots may reflect the community

412   present following historical coppicing or clearfelling for timber. Clearfelling results in

413   soil disturbance, more light reaching the ground (Ash & Barkham 1976; Collins &

414   Pickett 1988; Mitchell 1992) and an increased availability of colonisation sites,

415   leading to an increase in species richness through the dispersal of propagules into

416   clearfelled plots and/or regeneration from the seed bank (Roberts & Zhu 2002; Pykälä

417   2004). This is reflected in the species composition of clearfelled plots, which

418   contained many ruderal and grassland species such as *Chamerion angustifolium* (L.),

419   *Buddleja davidii* (Franch.) and *Ranunculus acris* (L.).

420

421   The woodland species composition of plantations, clearfelled or thinned plots did not

422   resemble the native plots. This is likely due to the age of native plots; they have

423   existed as native woodland for decades, or centuries, enabling the establishment of

424   slow colonising woodland species. There is no list of ancient woodland indicator

425   species for the Forest of Dean, but species such as *A. nemorosa*, *M. perennis*, and *Ilex*

426   *aquifolium* (L.), have been identified as ancient woodland species in other regions

427   (Hermy *et al.* 1999; Rose & O'Reilly 2006). While these species were present in

428   plantations, thinned plots, and clearfelled plots, they were more abundant in the native

429   plots. Continued monitoring is required to see if the woodland species composition of

430   clearfelled and thinned plots moves towards that of native plots.

431

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

433 The diversity of phytophagous invertebrates often follows that of the plant community

434 (Brown & Hyman 1986; Crisp, Dickinson & Gibbs 1998; Siemann, Haarstad &

435 Tilman 1999; Rowe & Holland 2013), and leaf-miner species richness did increase

436 with plant species richness on plantations, thinned and native plots. Most leaf-miners

437 are specialists on a small number of related host-plants (Memmott, Godfray & Gauld

438 1994). Therefore, as plant species richness increases more niches are available for

439 leaf-miner species, and more leaf-miner species are able to establish in the

440 community. However, greater plant species richness did not necessarily lead to

441 greater species richness of leaf-miners. On clearfelled plots leaf-miner species

442 richness did not increase as plant species richness increased, demonstrating that the

443 relationship between plant species richness and invertebrate herbivore species

444 richness can differ under different management regimes.

445

446 Although not measured here, clearfelled plots had greater, denser, vegetation cover

447 than the other plots. The vegetation cover on clearfelled plots may make it difficult

448 for leaf-miners to locate host plants in species rich communities using visual or

449 chemical cues (McNair, Gries & Gries 2000; Jactel *et al.* 2011; Dulaurent *et al.* 2012),

450 preventing them from establishing. This could occur through reduced resource

451 concentration, whereby herbivores are less able to find host plants when they do not

452 form dense stands (Root 1973), and/or reduced focal plant apparency, whereby

453 herbivores are less able to find host plants when they are concealed by taller non-host

454 plants (Floater & Zalucki 2000; Hughes 2012; Castagneyrol et al. 2013). When plant

455 species richness is lower, but the vegetation cover is high, these mechanisms will not

456 occur, and leaf-miners may be even more likely to establish due to the ease of locating

457   host plants when they form dense stands. Further investigation is needed to determine

458   if these mechanisms explain our results.

459

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

461   Forest type had no effect on leaf-miner species richness, but did affect the species

462   richness of the ground flora and richness of woodland species in the ground flora,

463   with mesotrophic *Fraxinus* plots having a greater species richness of both these

464   groups. However, there were no significant interactions between forest type and

465   management regime. Differences between the forest types are differences in the

466   number of species present and not in the patterns of species richness between

467   management regimes. This is important as it means that, for these two forest types at

468   least, the results from a study of the ground flora community on one forest type can be

469   applied to the other, saving time and money.

470

471   **Conclusions**

472   Both restoration methods conserved the woodland plant species richness of sites

473   during restoration. This has important management implications. Which restoration

474   method to use depends on many factors, but the results here suggest that both can be

475   considered. However, clearfelling may be the only option possible on sites that

476   cannot easily be visited multiple times for thinning, and these results suggest

477   that this will not be at the expense of the woodland ground flora. Clearfelling also

478   requires less time and money. We found that the method of restoration influenced the

479   relationship between plant and herbivore species richness. Therefore, species higher

480   up the food chain, such as herbivores, should also be monitored during restoration.

481   Restoration aims to restore the integrity of degraded systems, and this necessarily

482   involves observing more than just plant species.

483

484 **Acknowledgements**

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697 **Figures**
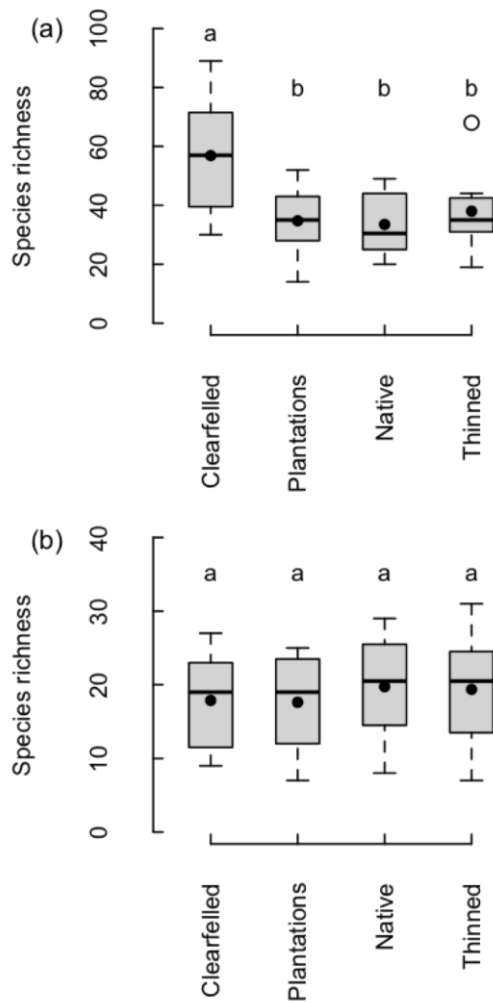
698

699 **Figure 1.** Plant species richness in the four types of plot: a) The total ground flora

700 species richness of plots under different management regimes; b) The woodland

701 ground flora species richness. Different letters within each panel indicate significant

702 differences (P < 0.0001).

703
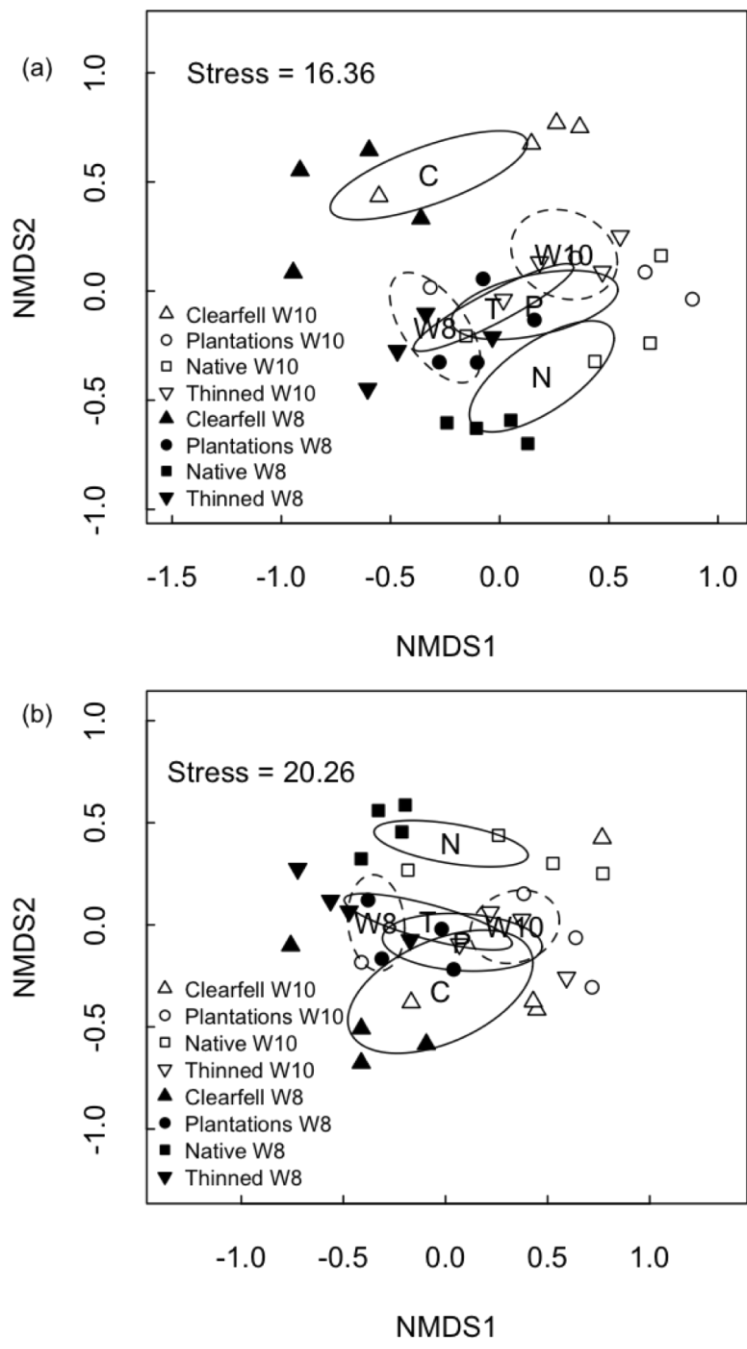
Figure 2. Nonmetric multidimensional scaling plot of the composition of the ground

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

plot. Ellipses represent 95% confidence intervals of the mean score of management

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

708
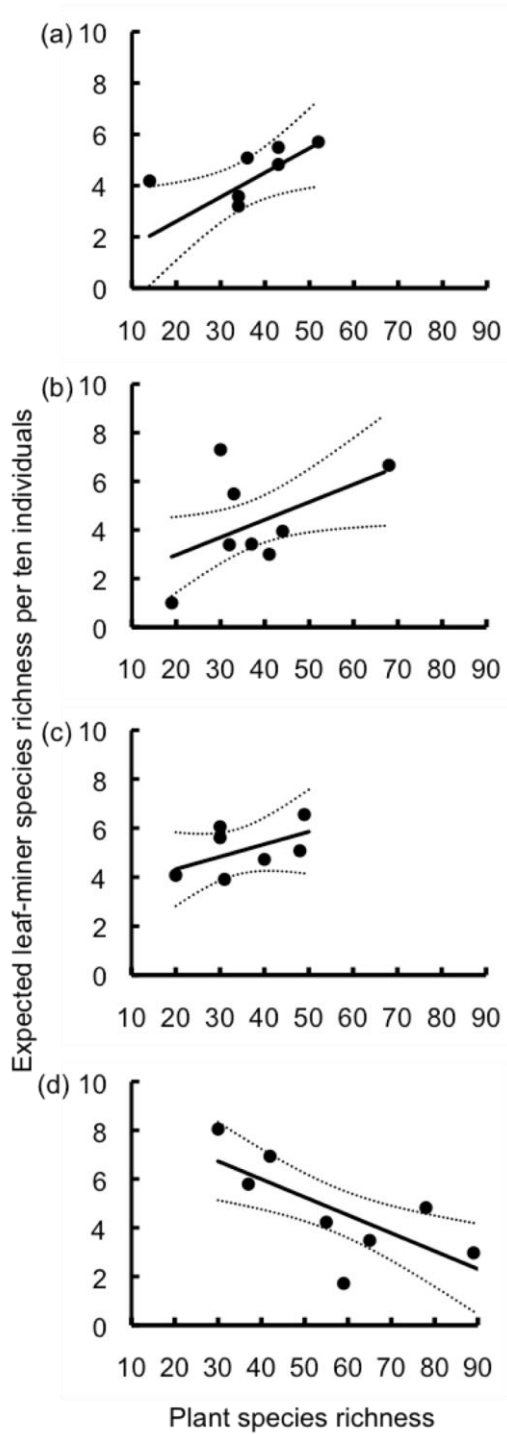
Figure 3. The relationship between plant species richness and rarefied leaf-miner

species richness for (a) plantations, (b) thinned plots, (c) native plots, and (d)

clearfelled plots. Dashed lines indicate 95% confidence intervals. The underlying

model is a general linear mixed model with site as a random effect.

713 **Supporting Information**

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

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

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

717 **Table S3.** Leaf-miner species found in the ground flora of study plots.