Epiphyte recovery following invasive plant control

1 **The epiphytic bryophyte community of Atlantic oak woodlands shows clear**

2 **signs of recovery following the removal of invasive *Rhododendron***

3 ***ponticum.***

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Abstract

Increased awareness of the negative impacts of invasive non-native species has led to a rapid increase in clearance programs around the world. One of the main goals of clearance is the restoration of native communities that were present pre-invasion. Little monitoring is typically carried out, however, to verify that native communities return without further management intervention in the years following invasive species removal. We investigated whether the epiphytic plant community of Atlantic oak woodlands, which principally consists of bryophyte species, returned after up to thirty years of recovery following the removal of the invasive non-native shrub *Rhododendron ponticum*. This community is of international conservation value and is particularly threatened by invasive *Rhododendron*. We revealed that the epiphytic plant community was able to recover effectively in sites that had been clear from *Rhododendron* for over fifteen years. This recovery included several species of particular conservation interest with highly restricted European distributions (i.e. 'Atlantic species' such as *Plagiochila heterophylla*). Total cover and species richness both returned to similar or even higher levels to those found in uninvaded control plots by fifteen or more years following clearance, despite being highly reduced within dense *Rhododendron* thickets. Overall community composition also recovered to resemble uninvaded control plots in the years following *Rhododendron* removal. These findings present an encouraging message that at least some native communities can return naturally in the years following invasive species removal and may not require further management interventions to speed their return.

40 **Keywords:** Atlantic oak woodland, bryophytes, epiphytes, invasive species,

41 restoration, *Rhododendron ponticum*.

42

43 **1. Introduction**

44   Invasive alien species are widely recognised as one of the major threats to

45 worldwide native biodiversity (Genovesi 2005; Mooney 2005). Whilst an

46 abundance of studies have investigated their impacts on aquatic communities,

47 small mammals, insects and vascular plants, their impact on bryophyte

48 communities has received little attention (Rothero 2003; Genovesi 2005;

49 Mooney 2005). Indeed, bryophytes remain a relatively overlooked element in

50 conservation strategies and their response to restoration measures is rarely

51 considered (Rothero 2003; Long and Williams 2007). Understanding how

52 bryophyte communities respond to invasive non-native species and revealing

53 whether they recover following control efforts will be vital to ensuring the future

54 of this diverse group (Rothero 2003; Long and Williams 2007).

55   The bryophyte community of Scottish Atlantic oak woodlands is

56 particularly rich and is recognised as being of internationally significant

57 conservation value (Rothero 2005; Long & Williams 2007; Porley and Hodgets

58 2005 pp164), as well as being listed in the EC Habitats Directive Annex 1 as "old

59 sessile oakwoods with *Ilex* and *Blechnum* in the British Isles" (JNCC 2014).

60 Invasion by non-native *Rhododendron ponticum* (hereafter *Rhododendron*) has

61 been identified as one of the main threats to this habitat, since the characteristic

62 humid climate and lack of temperature extremes which favour bryophyte

63 diversity are also ideal for *Rhododendron* growth (Porley & Hodgets 2005,

64 pp165; Rothero 2005). Whilst there is clear evidence that *Rhododendron*

65 invasion negatively impacts the understorey community (Cross 1975;

66 Rotherham 1983; Maclean *et al.* 2017), there is little quantitative evidence for

67 how it impacts the epiphytic community, including the diverse epiphytic

68 bryophyte assemblage (Long & Williams 2007). Equally little is known about

69 how this community responds to removal of the invasive stands, a practice which

70 has increased dramatically in recent years following the discovery that

71 *Rhododendron* serves as a host for *Phytophthera ramorum*, the fungus

72 responsible for sudden oak death in trees, which also presents a significant

73 economic threat to larch trees in Scotland (Edwards & Taylor 2008; Parrott &

74 MacKenzie 2013). Addressing this key knowledge gap and elucidating how the

75 epiphytic bryophyte community responds to *Rhododendron* invasion and

76 subsequent control is therefore of vital importance to assessing the efficacy of

77 Atlantic woodland conservation strategies (Long & Williams 2007; Parrott &

78 MacKenzie 2013).

79   Invasion by *Rhododendron* leads to a well-documented decline in native

80 understorey plant communities, which appears to be principally mediated

81 through reduced light intensity under the dense stands (Cross 1975, Maclean *et*

82 *al.* 2016). Since many epiphytic bryophytes are pre-adapted to low light

83 conditions, this may facilitate their persistence during invasion (Porley &

84 Hodgetts 2005 pp148; Kiraly et al. 2013). Additionally, it may be that epiphytic

85 species can persist higher up the tree trunk, above the most severe impacts of

86 the invading *Rhododendron,* leaving small source populations to recolonise down

87 tree trunks once the *Rhododendron* has been removed (Zartman 2003; Pharo &

88 Zartman 2006). The dense shading effect of *Rhododendron* is likely to be reduced

89 higher up the tree where light has less far to travel and can penetrate more easily

90 (Cross 1975). However, conditions higher up the trunk may be unsuitable

91 because of decreased humidity and increased exposure to temperature extremes

92 which may limit the ability of many epiphytic species to survive invasion by

93 retreating up the trunk in this manner (Porley & Hodgetts 2005). Indeed, since

94 mature *Rhododendron* bushes can attain heights of up to 8 m in wooded areas, it

95 is very possible that even epiphytes will be unable to tolerate their influence and

96 will become locally extinct in invaded areas (Edwards 2006). Many bryophytes

97 are reported to have limited dispersal capabilities, so it seems very likely that

98 once they have been lost in an area, recolonisation will take many decades (Miles

99 & Longton 1992; Snäll et al. 2003; Söderström & During 2005).

100 This study assessed the extent to which the epiphytic bryophyte

101 community of Atlantic oak woodland recovered following the effective removal

102 of invasive *Rhododendron* stands. To investigate this issue we utilised a series of

103 sites where dense *Rhododendron* stands had been removed between one and

104 thirty years ago. Using sites with up to thirty years of recovery following

105 *Rhododendron* removal to allow us to investigate the long-term consequences of

106 invasive species removal over ecologically relevant timescales. We used this

107 series of sites to address the questions: in the years following *Rhododendron*

108 clearance 1) does the total cover and species richness of the epiphytic plant

109 community return to levels similar to those found in uninvaded control sites?; 2)

110 does community composition return to a similar structure to that found in

111 uninvaded control sites?; and 3) do Atlantic species (which have highly restricted

112 European distributions and are of particular conservation importance) also

113 recover?

114

2. Methods

2.1 Data Collection

We identified and surveyed a series of 32 sites that were previously invaded by high density *Rhododendron* stands, but which had been cleared at different points in time between 1984 and 2013. We also surveyed 16 high *Rhododendron* density sites that have never been cleared and 16 uninvaded control sites for comparison with the cleared sites. Potential sites were identified following discussions with personnel at the regional Scottish Natural Heritage and Forestry Commission Scotland offices and meetings with local landowners with a substantial *R. ponticum* presence on their properties. Sites were chosen based on availability and also to ensure the even distribution of site types throughout the study area. Particular care was taken to ensure that dense *Rhododendron* and uninvaded control sites were fully interspersed with the cleared sites. This study design therefore conformed to the 'natural experiment' paradigm described by Diamond (1983), whereby site locations for experimental treatments (in this case uninvaded, dense or cleared *Rhododendron)* are determined by availability rather than following a strict experimental design with perfectly interspersed plots. This type of study is implemented due to constraints on conducting a strict experimental trial to answer the question under consideration (in this case the time constraint on the many decades necessary to grow and clear *Rhododendron* in an ideally designed field trial).

Sites were chosen to be as similar as possible to reduce variability not associated with their history of *Rhododendron* invasion. All survey sites were located on the west coast of Scotland in Atlantic oak woodlands around Argyll,

139   Kintyre and Lochaber, between 55°76' N and 56°90'. Atlantic oak woodlands are

140   of high biodiversity value and are listed in Annex I of the EU Habitats Directive

141   (old sessile oak woods with *Ilex* and *Blechnum* in the British Isles). Oak (*Quercus*

142   *petraea* [Mattuschka] and *Q. robur* [Mattuschka]), and birch (*Betula pendula*

143   [Roth] and *B. pubescens* Ehrh.) made up the majority of the tree community at all

144   sites, with rowan (*Sorbus acuparia* L.), hazel (*Corylus avellana* L.), ash (*Fraxinus*

145   *excelsior* L.), and holly (*Ilex aquifolium* L.) also occurring in moderate

146   abundances. All sites consisted of ancient semi-natural woodland and were

147   located more than 100 m from any ravines or plantation forestry and none were

148   subject to active management of the tree community (i.e. no harvesting,

149   coppicing or removal of dead wood). *Rhododendron* was removed from all the

150   cleared sites by cutting the *Rhododendron* bushes at the base and applying

151   herbicide (usually triclopyr or glyphosate; Edwards 2006), which represents the

152   most common method of control currently used in Scotland (Edwards 2006).

153   *Rhododendron* clearance was periodically maintained at all sites to prevent its

154   return; however, no additional management interventions were applied at the

155   sites.

156   At each site we established a 20 m by 20 m plot to sample the epiphyte

157   community. It was decided to sample from this defined, limited area, rather than

158   using randomly selected trees dispersed throughout the entire woodland site in

159   order to keep the survey area the same between different sites and to ensure

160   that the entire survey plot had been subject to dense *Rhododendron* cover prior

161   to clearance. Dense *Rhododendron* cover was defined as being a mature stand

162   featuring closed canopy cover across the survey plot. For cleared sites, specific

163   plot locations within the greater woodland site were located following

7

164 discussions with the local land manager who could identify areas that had been

165 subject to suitably dense *Rhododendon* cover prior to clearance.

166   To sample the epiphyte community, we randomly selected nine oak and

167 nine birch trees within each plot to serve as sample trees. At a limited number of

168 sites we were unable to identify nine trees of each species within the survey plot,

169 in which case we extended the survey area to a 30 m by 30 m range. On the

170 North-facing side of each sample tree we placed a 30 cm tall by 10 cm wide mini-

171 quadrat at the base of the tree and also at breast height and recorded the total

172 percent cover of every plant species present in the quadrat (principally mosses

173 and liverworts, but occasionally including ferns and vascular species, especially

174 at the tree base). Only the North-facing side of the trees was surveyed in order to

175 maintain consistency between different trees, since the North side typically has a

176 higher bryophyte abundance than the South side (Porley and Hodgets 2005). We

177 therefore gathered survey data for four separate 'quadrat-types': birch at the

178 tree base (birch lower), birch at breast height (birch upper), oak at the tree base

179 (oak lower) and oak at breast height (oak upper).

180   Sites were split across ten spatial blocks with each block containing

181 cleared, dense and uninvaded control sites. All surveys were conducted during

182 summer 2014, apart from 13 uninvaded control site surveys and 11 dense

183 *Rhododendron* surveys, which were conducted in summer 2013. These surveys

184 were carried out in an identical manner and were used to supplement the 2014

185 dataset to maximise the uninvaded control and dense *Rhododendron* data that

186 were available for analysis.

187

188 *2.2 Statistical Analysis*

189   Community composition data were averaged across the nine quadrats per

190   plot for each of the four quadrat-types, generating plot-level data for further

191   analysis. Total percent cover (sum of the percent cover for all species in the

192   quadrat) was also averaged across the nine quadrats per quadrat-type in each

193   plot. Species richness, however, was cumulatively summed across the nine

194   quadrats to give the total number of species recorded in each plot for each

195   quadrat-type. Total percent cover and species richness data were also calculated

196   for mosses only and liverworts only in addition to the calculations for all species

197   together.

198   Mixed effect models using spatial block as a random effect were then

199   fitted using the nlme package (Pinheiro *et al.* 2014) in R statistical software

200   (version 3.1.2; R Core Team 2014) to test the effect of *Rhododendron* site type

201   (dense *Rhododendron*, recently cleared sites (1-14 years since clearance), older

202   cleared sites (15-30 years since clearance) and uninvaded control sites on 1)

203   total percent cover and 2) species richness. Tukey's HSD was also calculated for

204   each of these comparisons to reveal which of the site types were significantly

205   different.

206   To investigate changes to overall community composition, partial-

207   Redundancy Analyses (partial-RDA, incorporating spatial block as a random

208   effect) were carried out for each quadrat-type using CANOCO 5 statistical

209   software (ter Braak & Šmilauer 2012). Since the data covered only a short

210   gradient of community composition, linear methods (rather than unimodal

211   methods) were used. Permutation tests (using 9999 permutations) were used to

212   test the significance of all constrained axes and data for each plot were

213   standardised by plot norm so that the analysis would reveal changes in the

214 proportion of each species and not be unduly influenced by changes in total

215 vegetation cover between plots (Šmilauer & Lepš 2014). The same

216 *Rhododendron* site types as in the previous analysis were used as a categorical

217 explanatory variable (dense *Rhododendron*; uninvaded control; sites cleared 1-

218 14 years ago; and sites cleared 15-30 years ago). A classified plot diagram (ter

219 Braak & Šmilauer 2012) was then used to compare the community composition

220 of plots falling into each *Rhododendron* site type to discover whether community

221 composition was returning to that found in uninvaded control plots as time since

222 *Rhododendron* clearance increased.

223   A second set of analyses was then carried out using data for Atlantic

224 species only (following Hill & Preston 1998), in order to focus in on the response

225 of these species of particular conservation interest. Mixed models and Tukey's

226 HSD were utilised to investigate differences in total cover and species richness

227 with *Rhododendron* site type. The Atlantic species present in our surveys were:

228 mosses – *Dicranodontium denudatum* and *Dicranum scottianum*; liverworts -

229 *Bazzania trilobata; Drepanolejeunea hamatifolia; Frullania tennerifae;*

230 *Harpalejeunea molleri; Lejeunea patens; Lepidozia cupressina; Leptoscyphus*

231 *cuneifolius; Microlejeunea ulcina; Plagiochila exigua; Plagiochila heterophylla;*

232 *Plagiochila punctata; Plagiochila spinulosa* and *Scapania gracilis*, and ferns -

233 *Hymenophyllum tunbrigense* and *Hymenophyllum wilsonii.* Whilst the 'Atlantic

234 species' designation is typically limited to bryophytes, it was decided to include

235 the two filmy ferns in our analysis since they have similar distributions to the

236 Atlantic bryophytes and are considered species of interest in Atlantic oak

237 woodland (Long & Williams 2007). A species-enivronmental variables (i.e.

238 *Rhododendron* site type) biplot was then created from the previously constructed

239 RDA to look at the response of Atlantic community composition to *Rhododendron*

240 clearance. Whilst this analysis utilised data for all species (so that the complete

241 community would be taken into account when calculating the relationships

242 between plots in each treatment), only Atlantic species were then highlighted in

243 the resulting graph to reveal how they responded to *Rhododendron* clearance.

244

245 **3. Results**

246   Over the entire study, 63 different species were recorded, comprising 29

247 species of moss, 26 liverworts, 3 ferns and 5 vascular species (vascular species

248 were very occasionally present in quadrats located at the tree base). A total of 55

249 species were recorded on birch trees and a total of 59 species on oak trees.

250 Average percent cover across the study was 66%, with an average of 62% for

251 birch lower quadrats, 51% for birch upper quadrats, 82% for oak lower quadrats

252 and 71% for oak upper quadrats.

253

254 *3.1 Question 1: Does the total cover and species richness of the epiphytic plant*

255 *community return to similar levels found in uninvaded control sites?*

256   Overall percent cover did not show any significant differences between

257 the *Rhododendron* site types for birch lower ($F_{3,51} = 2.52$, $P = 0.069$), birch upper

258 ($F_{3,51} = 1.22$, $P = 0.313$) or oak upper ($F_{3,51} = 1.53$, $P = 0.219$) quadrats, but

259 recently cleared sites were revealed to have a lower epiphyte cover than

260 uninvaded control sites for oak lower quadrats ($F_{3,51} = 3.44$, $P = 0.023$) (Fig. 1).

261 Separate analyses of moss and liverwort cover, however, revealed that

262 significant changes in liverwort cover were being masked by opposing changes

263 in moss cover to result in this lack of change in the percent cover of all species

264   for most quadrat types. Tukey's HSD revealed that dense sites had significantly

265   lower liverwort cover than uninvaded control sites for both birch ($t_{3,51}$ = 3.10, P

266   = 0.016) and oak ($t_{3,51}$ = 3.29, P = 0.010) lower quadrats, but not for the upper

267   quadrats (birch: $t_{3,51}$ = 0.71, P = 0.891; oak: $t_{3,51}$ = 1.23, P = 0.610). Recently

268   cleared sites did not have significantly different liverwort cover from dense sites

269   (birch lower: $t_{3,51}$ = 1.16, P = 0.653; birch upper: $t_{3,51}$ = 0.28, P = 0.992; oak lower:

270   $t_{3,51}$ = 0.78, P = 0.862; oak upper: $t_{3,51}$ = 0.16, P = 0.877), but older cleared sites

271   (15 – 30 years since clearance) had a significantly higher liverwort cover than

272   dense sites for all four quadrat types (birch lower: $t_{3,51}$ = 6.16, P < 0.001; birch

273   upper: $t_{3,51}$ = 3.17, P = 0.013; oak lower: $t_{3,51}$ = 5.59, P < 0.001; oak upper: $t_{3,51}$ =

274   4.07, P < 0.001). Indeed, older cleared sites attained a significantly higher

275   liverwort cover than uninvaded control sites all quadrat types apart from oak

276   lower (birch lower: $t_{3,51}$ = 3.25, P = 0.011; birch upper: $t_{3,51}$ = 4.16, P < 0.001; oak

277   lower: $t_{3,51}$ = 2.02, P = 0.194; oak upper: $t_{3,51}$ = 2.67, P = 0.049). Whilst the glms

278   revealed no significant differences for moss cover in any quadrat type (birch

279   lower: $F_{3,51}$ = 1.99, P = 0.128; birch upper: $F_{3,51}$ = 1.37, P = 0.261; oak lower: $F_{3,51}$

280   = 1.50, P = 0.225; oak uper: $F_{3,51}$ = 1.83, P = 0.153), the general pattern was for

281   dense sites to have the highest cover, followed by uninvaded control sites, with

282   both recent and older cleared sites having the lowest cover. These trends were

283   opposite to the significant differences observed in liverwort cover and suggest

284   that the lack of change in overall cover masked the replacement of mosses with

285   liverworts as time since *Rhododendron* removal increased.

286   Analysis of differences in epiphyte species richness revealed very similar

287   patterns to those found for percent cover (Fig. 2). Tukey's HSD revealed that

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288 older cleared sites showed significantly higher liverwort species richness than

289 dense *Rhododendron* sites (birch lower: $t_{3,51}$ = 5.58, P < 0.001; birch upper: $t_{3,51}$ =

290 3.05, P = 0.019; oak lower: $t_{3,51}$ = 3.91, P = 0.002; oak upper: $t_{3,51}$ = 3.44, P =

291 0.006), whereas recently cleared sites were not significantly different from dense

292 sites for all four quadrat types (birch lower: $t_{3,51}$ = 1.78, P = 0.294; birch upper:

293 $t_{3,51}$ = 1.46, P = 0.467; oak lower: $t_{3,51}$ = 0.31, P = 0.781; oak upper: $t_{3,51}$ = 1.15, P =

294 0.663). Older cleared sites also showed significantly higher liverwort species

295 richness than uninvaded control sites for both lower quadrats (birch: $t_{3,51}$ = 3.08,

296 P = 0.017; oak: $t_{3,51}$ = 3.51, P = 0.005), but not the upper quadrats (birch: $t_{3,51}$ =

297 2.04, P = 0.188; oak: $t_{3,51}$ = 1.46, P = 0.469). Again, the glms revealed no

298 significant differences in moss species richness between *Rhododendron* site types

299 (birch lower: $F_{3,51}$ = 0.69, P = 0.561; birch upper: $F_{3,51}$ = 1.35, P = 0.268; oak

300 lower: $F_{3,51}$ = 2.05, P = 0.119; oak upper: $F_{3,51}$ = 0.40, P = 0.749), but in contrast to

301 the percent cover analyses, this did not act in opposition to the trends in

302 liverwort species richness, resulting in significant differences in overall epiphyte

303 species richness between the different *Rhododendron* site types for all four

304 quadrat types (birch lower: $F_{3,51}$ = 5.24, P = 0.003; birch upper: $F_{3,51}$ = 5.03, P =

305 0.004; oak lower: $F_{3,51}$ = 6.05, P = 0.001; oak upper: $F_{3,51}$ = 2.78, P = 0.049).

306

307 *3.2 Question 2: Does community composition return to a similar structure to that*

308 *found in uninvaded control sites?*

309   The partial-RDAs (Fig. 3) demonstrated a significant impact of

310 *Rhododendron* site type on epiphyte community composition (birch lower: F =

311 3.3, P < 0.001; birch upper: F = 2.1, P = 0.002; oak lower: F = 2.3, P = 0.002; oak

312 upper: F = 1.9, P = 0.006). They revealed that community composition in

313 uninvaded control plots (UC) was predictably different from that in dense

314 *Rhododendron* plots (DR). However, there was a degree of overlap in the space

315 occupied by plots belonging to these two groups in the diagrams, revealing that

316 many similarities remain between the epiphyte community in dense

317 *Rhododendron* and uninvaded control plots. The analyses also revealed a definite

318 recovery in community composition as time since *Rhododendron* control

319 increased, with plots cleared less than 15 years ago largely occurring to the right

320 of the diagrams, close to the dense *Rhododendron* plots, and plots cleared 15 to

321 30 years ago largely occurring to the left of the diagrams, close to the uninvaded

322 control plots. However, there was substantial overlap between the different

323 groups, demonstrating that although community composition did change as time

324 since *Rhododendron* clearance increased, the different communities were still

325 fairly similar and there was not a complete turnover in community composition

326 between the different plot types.

327

328 *3.3 Question 3: Do Atlantic species recover as readily as more widely distributed*

329 *species?*

330   A complete list of all the Atlantic species present in each *Rhododendron*

331 site type is available in the Supporting Information (Tables S1 and S2). The glms

332 revealed that *Rhododendron* site type had a significant impact on the percent

333 cover and species richness of Atlantic species for all four quadrat types (percent

334 cover: birch lower: $F_{3,51}$ = 7.94, P < 0.001; birch upper: $F_{3,51}$ = 3.19, P = 0.031; oak

335 lower: $F_{3,51}$ = 8.17, P < 0.001; oak upper: $F_{3,51}$ = 3.85, P = 0.015: species richness:

336 birch lower: $F_{3,51}$ = 10.02, P < 0.001; birch upper: $F_{3,51}$ = 3.74, P = 0.017; oak

337   lower: $F_{3,51}$ = 7.35, P < 0.001; oak upper: $F_{3,51}$ = 6.61, P < 0.001) (Fig. 4). Tukey's

338   HSD revealed that recently cleared sites were not significantly different from

339   dense *Rhododendron* sites for either percent cover (birch lower: $t_{3,51}$ = 1.06, P =

340   0.715; birch lower: $t_{3,51}$ = 0.83, P = 0.839; oak lower: $t_{3,51}$ = 0.33, P = 0.879; oak

341   upper: $t_{3,51}$ = 0.44, P = 0.862) or species richness (birch lower: $t_{3,51}$ = 1.85, P =

342   0.265; birch upper: $t_{3,51}$ = 1.78, P = 0.296; oak lower: $t_{3,51}$ = 0.78, P = 0.763; oak

343   upper: $t_{3,51}$ = 1.12, P = 0.680). Older cleared sites, however, showed significantly

344   higher percent cover (birch lower: $t_{3,51}$ = 4.66, P < 0.001; birch upper: $t_{3,51}$ = 2.94,

345   P = 0.025; oak lower: $t_{3,51}$ = 4.39, P < 0.001; oak lower: $t_{3,51}$ = 2.75, P = 0.035) and

346   species richness (birch lower: $t_{3,51}$ = 5.42, P < 0.001; birch upper: $t_{3,51}$ = 3.33, P =

347   0.009; oak lower: $t_{3,51}$ = 3.92, P = 0.002; oak upper: $t_{3,51}$ = 4.14, P < 0.001) than

348   dense sites, suggesting that Atlantic species recovered well following the

349   removal of invasive *Rhododendron*. Indeed, for birch lower quadrats, older

350   cleared sites actually attained a higher Atlantic species richness than uninvaded

351   control sites ($t_{3,51}$ = 3.02, P = 0.020), and this pattern was repeated for the other

352   quadrat types, though the differences were not significant (birch upper: $t_{3,51}$ =

353   1.77, P = 0.298; oak lower: $t_{3,51}$ = 1.19, P = 0.638; oak lower: $t_{3,51}$ = 1.43, P =

354   0.488).

355   The partial-RDAs (Fig. 5) revealed that Atlantic species had a strong

356   aversion to dense *Rhododendron* plots (DR) and were more likely to be found in

357   uninvaded control (UC) and cleared (1-14 and 15-30) plots for all quadrat types

358   apart from birch upper, which did feature several Atlantic species in the dense

359   *Rhododendron* plots. An affinity of *Drepanolejeunea hamatifolia* for dense

360   *Rhododendron* plots was also observed in the oak lower quadrats. The centroid

361   for uninvaded control (UC) and older cleared plots (15-30) were very close for

362   the lower quadrats, highlighting that these site types feature very similar

363   communities and that recovery has been largely successful. These centroids

364   were further apart for the upper quadrats (though still at the same side of the

365   diagram), suggesting that recovery has been less complete in these quadrats.

366   However, this may also be driven by the larger degree of overlap between

367   recently cleared sites (1-14) and uninvaded controls for these upper quadrats

368   (Fig. 3).

369

370   **4. Discussion**

371   The epiphytic plant community, which was principally comprised of

372   bryophytes, recovered well in the years following *Rhododendron* clearance,

373   showing substantial increases in both total vegetation cover and species richness

374   by 15 to 30 years following clearance. This recovery applied equally to Atlantic

375   species as to more widespread species. Ordinations revealed that whilst dense

376   *Rhododendron* caused a slight shift in community composition away from that

377   found in uninvaded control plots, the community appeared to be reconverging

378   on the composition found in uninvaded control plots after 15 to 30 years of

379   recovery following effective *Rhododendron* clearance. These results therefore

380   suggest that epiphytic plants of Scottish Atlantic oak woodlands are relatively

381   resilient to the long-term effects of invasive *Rhododendron*. Whilst invaded sites

382   showed reductions in epiphytic plant species richness, cleared sites could be,

383   ultimately, as rich and diverse as pristine, uninvaded woodlands.

384

385 *4.1 Question 1: Does the total cover and species richness of the epiphytic plant*
386 *community return to similar levels found in uninvaded control sites?*

387 *Rhododendron* invasion had unexpectedly little impact on the overall
388 percent cover of epiphytic species, with no significant differences being found
389 between densely invaded plots, older cleared plots and uninvaded controls.
390 Greater impacts were observed for species richness than for percent cover,
391 however, with older cleared sites having significantly higher species richness
392 than densely invaded sites. Whilst dense plots were revealed to have lower
393 species richness than uninvaded controls, these differences were not significant
394 due to considerable variation between plots of the same *Rhododendron* type. This
395 lack of a significant difference between dense and uninvaded plots for both cover
396 and species richness was surprising given the dramatic decreases in the cover of
397 understorey species during *Rhododendron* invasion (Cross 1975; Maclean *et al.*
398 2017), and the high concern in the conservation literature that *Rhododendron*
399 invasion is detrimental to epiphytic bryophytes (Long and Williams 2007). Since
400 epiphytic bryophytes are typically adapted to the reduced light levels and higher
401 humidity found under tree canopies, it may be that they are better able to
402 survive further light reductions caused by invasive shrubs compared to the
403 vascular species examined in most studies (Porley & Hodgets 2005 pp148; Kiraly
404 *et al.* 2013; Maclean *et al.* 2017). Indeed, there are concerns that the dramatic
405 changes to light intensity and humidity caused by removing the invasive
406 *Rhododendron* stands may damage any surviving bryophytes (Long & Williams
407 2007; see also Dynesius & Hylander 2007). Whilst leaving dead *Rhododendron*
408 stems in place may help to mitigate this impact and facilitate restoration (Long &
409 Williams 2007; Parrott & MacKenzie 2013), our study revealed that even in the

410 absence of these enhanced management measures, the epiphytic bryophyte

411 community was able to recover well in 15 to 30 years.

412   Partitioning the results to look separately at mosses and liverworts,

413 revealed that large impacts to liverwort cover and species richness were being

414 partially masked by reduced impacts on mosses. Liverworts showed significantly

415 lower cover in dense than uninvaded plots for the lower quadrats. They also

416 underwent dramatic increases in both cover and species richness with

417 increasing time since *Rhododendron* clearance, with older cleared sites (15-30

418 years) featuring the same or higher cover and species richness than uninvaded

419 controls. This higher liverwort cover and species richness in plots with 15-30

420 years since clearance than in uninvaded control plots was surprising. It may be

421 that some feature of cleared sites, such as a lack of competition with vascular

422 plants, particularly at the tree base, may have benefitted the liverwort

423 communities. Alternatively, it may be that our uninvaded control sites were not

424 as directly comparable with our cleared sites as hoped. Whilst a great deal of

425 care was taken to select sites that would be directly comparable, it may be that

426 certain features that facilitated *Rhododendron* growth, such as high humidity,

427 also made these sites particularly favourable to liverwort growth. Since it is

428 impossible to know what communities were present at these sites prior to

429 invasion (which occurred many decades ago), comparison with uninvaded sites

430 represented the only available baseline against which to assess recovery. In any

431 case, the high liverwort cover and species richness at older cleared sites

432 highlights the conservation potential of these areas and emphasises the

433 importance of ensuring that cleared sites remain *Rhododendron*-free.

434   The rapid recovery in liverwort species richness indicated that, whilst

435   dense *Rhododendron* stands were detrimental to liverwort cover, species were

436   able to quickly recover their former abundance following clearance. It is possible

437   that the native liverworts were able to persist higher up the tree during invasion,

438   so avoiding the most severe impacts of the *Rhododendron*. Similar niche shifts

439   along canopy height were seen following the disturbance caused by forest

440   fragmentation in Amazonian forests (Zartman 2003; Pharo & Zartman 2006).

441   The higher liverwort cover in upper quadrats than lower quadrats in dense

442   *Rhododendron* plots found in our study would support the presence of upper

443   canopy refugia, but unfortunately logistical constraints precluded sampling high

444   into the canopy. In addition to surviving higher up the trees, small pockets of

445   diversity may have persisted on individual trees growing in small gaps in the

446   invasive *Rhododendron* thickets. Whilst we know of no other studies addressing

447   the impact of invasive plants on epiphyte diversity, studies considering the

448   impacts of other disturbances such as forest fragmentation and clear-felling

449   showed mixed benefits of small, isolated refugia, with beneficial effects

450   demonstrated in some studies (Dynesius & Hylander 2007; Toledo-Aceves *et al.*

451   2014), and no benefit shown in other cases (Lohmus, Rosenvald & Lohmus 2006;

452   Perhans *et al.* 2009).

453   Whilst all our cleared plots were located in areas that originally hosted

454   very dense *Rhododendron* stands, the total extent and configuration of these

455   stands will undoubtedly have differed with respect to their ability to provide

456   effective refugia. This variation in the presence of refugia, or in the distance to

457   the nearest uninvaded woodland, may explain much of the variation seen in our

458   results between plots in the same *Rhododendron* category. Another potential

459   source of variation may have been the duration of invasion prior to clearance,

460   which was always long enough to provide mature, dense *Rhododendron* cover,

461   but may have differed by several years or decades between sites. Unfortunately

462   the lack of a detailed history of *Rhododendron* spread at the majority of sites

463   prevented using this information as an additional explanatory variable in our

464   analyses.

465   Mosses, in contrast to liverworts, showed very few significant changes

466   through time, and did not demonstrate uncharacteristically low levels of cover or

467   species richness in the dense *Rhododendron* plots. This suggested that they were

468   better able to persist under the dense *Rhododendron* stands and maintain typical

469   levels of cover during the invasion. Observations in the field supported these

470   findings, with trees under dense *Rhododendron* canopy often featuring a

471   moderate cover of common mosses such as *Isothecium myosuroides* or *Hypnum*

472   *cupressiforme*. Whilst these populations were typically etiolated and pale and

473   rarely bore sporophytes (J. Maclean, pers. obs.), it seems they served to

474   effectively maintain a foothold for many species in the face of invasion.

475

476   4.2 Question 2: *Does community composition return to a similar structure to that*

477   *found in uninvaded control sites?*

478   Ordination revealed that the community composition of epiphytic plants

479   in plots where *Rhododendron* was cleared 15 to 30 years ago was very similar to

480   that of uninvaded control plots, suggesting that site recovery had been largely

481   successful. This recovery was particularly effective for the lower quadrats,

482   although substantial overlap was also detected between cleared sites and

483   uninvaded control sites for the upper quadrats. Oak upper quadrats in particular

484   may require a longer period of recovery to achieve the community composition

485   found in uninvaded controls. Differences in community composition, however,

486   were fairly slight, even between uninvaded control and dense *Rhododendron*

487   plots, which exhibited some degree of overlap in all four quadrat types (birch

488   and oak, tree base and breast height). A relatively short gradient in community

489   composition (between 2.1 and 2.7 units), which supported the use of linear

490   rather than univariate ordination techniques, also suggested that the plots did

491   not exhibit a high degree of community turnover and had many species in

492   common. This similarity in the epiphytic community between dense, cleared and

493   uninvaded sites contrasts the large differences seen in the understorey

494   community and emphasises that different communities within a site may

495   respond very differently to both the arrival and the removal of invasive species

496   (Maclean *et al.* 2017).

497   The successful recovery of native species following invasive species

498   removal is a relatively rare occurrence (Reid *et al.* 2009; Corbin & D'Antonio

499   2012), although it has been reported in some cases (Patten & O'Casey 2007; Rey

500   Benayas *et al.* 2009). To our knowledge, this is the first study to investigate the

501   impact of invasive plant removal on the native epiphyte community, and it was

502   encouraging to discover a healthy native epiphytic plant community in sites that

503   had been *Rhododendron*-free for at least 15 years. It should be noted that we only

504   recorded plant species in our surveys and did not monitor other important

505   components of the epiphytic community such as lichens. Further study will be

506   necessary to reveal how lichens respond to *Rhododendron* invasion and

507   clearance and it cannot be assumed that they will show the same patterns of

508   recovery as the species investigated in this study. Since the majority of the

21

509 epiphytic plant community in our study area consisted of bryophytes

510 (supplemented by some ferns and a few understory vascular species at the tree

511 base), this recovery relied on the ability of bryophytes to survive the invasion in

512 low numbers and increase their populations effectively after the *Rhododendron*

513 had been cleared. This ability of bryophytes to recover following *Rhododendron*

514 clearance is supported by research revealing that bryophytes in the understorey

515 also recover well following *Rhododendron* clearance, whereas forbs and grasses

516 do not (Maclean *et al.* 2017).

517   As discussed in the previous section, it is possible that small bryophyte

518 populations were able to persist in refugia higher up the trees, or on isolated

519 trees growing in spots of reduced *Rhododendron* density (Zartman 2003;

520 Dynesius & Hylander 2007). The ability of epiphytic bryophytes to increase their

521 populations and spread rapidly from such refugia is a highly debated topic

522 (Pharo & Zartman 2007). Studies that directly measure spore dispersal have

523 found that a vast majority of spores remain within a few centimetres of the

524 parent plant (Miles & Longton 1992; Porley & Hodgets 2005), and bryophytes

525 are typically reported as being highly dispersal limited (Snäll *et al.* 2003;

526 Söderström & During 2005). This, however, runs in contrast to evidence that

527 bryophytes can occasionally disperse very long distances, giving rise to

528 distributions that span multiple continents (Porley & Hodgets 2005 pp74; Pharo

529 & Zartman 2007). Additionally, some studies have discovered high rates of

530 community turnover, for example discovering large differences in bryophyte

531 community composition between different seasons of the same year, which

532 suggest an ability to spread rapidly when conditions are favourable (Scott 1971;

533 Ross-Davis & Frego 2004). Indeed, the ability of most bryophytes to reproduce

534 by forming a new plant from a detached fragment of leaf or stem, in addition to

535 the production of sexual spores or specialised asexual propagules (gemmae), is

536 likely to facilitate their ability to spread over moderate distances (Porley &

537 Hodgets pp77). Altogether, our results showing a healthy community 15-30

538 years after removal suggests that most species were able to recover effectively

539 and increase their coverage in the years following *Rhododendron* removal.

540

541

542 *4.3 Question 3: Do Atlantic species recover as readily as more widely distributed*

543 *species?*

544   The Atlantic species present in our study (incorporating two mosses,

545 thirteen liverworts and two filmy ferns) showed dramatic increases in both total

546 cover and species richness as time since *Rhododendron* clearance increased.

547 These increases culminated in plots where *Rhododendron* was cleared 15 or

548 more years ago achieving levels of cover and species richness that were

549 indistinguishable from, or in the case of birch lower species richness,

550 significantly higher than, uninvaded control plots. The partial-RDA revealed that

551 Atlantic species were present in their highest abundances in cleared and

552 uninvaded plots, and the similarity between older (15-30 years) cleared and

553 uninvaded plots suggested that Atlantic species were able to recover following

554 *Rhododendron* removal, particularly in the lower quadrats (Fig. 5). In contrast,

555 dense *Rhododendron* was highly unfavourable to Atlantic species, with the

556 vectors for almost all Atlantic species clustering away from the dense

557 *Rhododendron* plots, although some appeared to show an affinity for the dense

558 *Rhododendron* plots in birch upper quadrats. It is therefore clear that

23

559 *Rhododendron* invasion was highly detrimental to Atlantic bryophytes, although

560 its effective removal appears sufficient to counter much of its negative impact

561 and further management interventions are unlikely to be required for the

562 species present in our study.

563   Our results have revealed that the Atlantic species in our dataset, which

564 consisted principally of liverworts, responded to *Rhododendron* removal in a

565 similar way to the liverwort community as a whole. Since Atlantic species are

566 defined by their distribution rather than on ecological grounds, there would be

567 no strong reason to expect them to respond any differently from non-Atlantic

568 species to disturbances such as plant invasions (Ratcliffe 1968; Porley & Hodgets

569 2005 pp83). However, since an Atlantic distribution is in most cases

570 underpinned by a requirement for relatively consistent moisture availability

571 throughout the year (Ratcliffe 1968; Porley & Hodgets 2005 pp83), it could be

572 supposed that Atlantic species would be more vulnerable to the rapid changes in

573 humidity caused by removing dense *Rhododendron* thickets (Long & Williams

574 2007). Indeed, invasive *Rhododendron* has often been cited as one of the major

575 threats to Atlantic bryophyte conservation, but critical information on their

576 recovery following *Rhododendron* clearance was lacking (Long & Williams 2007;

577 Scottish Natural Heritage 2007; Edwards & Taylor 2008). It is therefore highly

578 encouraging that our study has revealed that Atlantic species recover well

579 following *Rhododendron* clearance, so long as the site remains *Rhododendron*-

580 free. We wish to highlight, however, that we used general, untargeted surveys in

581 our analysis and only monitored oak and birch trees due to the logistical

582 constraints of monitoring all the tree species present in Atlantic oak woodland.

583 These surveys therefore capture only the responses of regionally abundant

584 epiphytes of oak and birch and further targeted surveys will be necessary to fully

585 assess the impact of *Rhododendron* invasion on rare species of particular

586 conservation interest. It was encouraging to find *Plagiochila heterophylla* in one

587 cleared and two dense *Rhododendron* plots (in addition to three uninvaded

588 controls), however, suggesting that this rare though locally frequent Atlantic

589 bryophyte can still be found following *Rhododendron* invasion.

590

591

592 *4.4 Conclusions*

593   Invasive *Rhododendron* stands cause widely reported declines in native

594 plant communities (Cross 1975; Rotherham 2001; Scottish Natural Heritage

595 2007). Whilst most previously published scientific research has focussed on

596 impacts to vascular plants (see for example Cross 1975; Rotherham 1983; Nilsen

597 *et al.* 2001; Maclean *et al.* 2017), our study supports abundant qualitative

598 observations that dense *Rhododendron* causes a decrease in the cover and

599 species richness of epiphytic bryophytes, with liverworts being particularly

600 affected (Long & Williams 2007; Parrott & MacKenzie 2013). Our research went

601 further, however, to investigate for the first time how the native epiphytic plant

602 community responded to the removal of this invasive shrub. We revealed that

603 total cover and species richness increased dramatically in the years following

604 *Rhododendron* removal, with overall community composition recovering

605 successfully to resemble that of uninvaded control plots. Altogether, our results

606 provide a message of encouragement that this important component of

607 internationally renowned Atlantic oak woodlands is able to recover without any

608   further   management   interventions   following   the   removal   of   invasive

609   *Rhododendron.*

610

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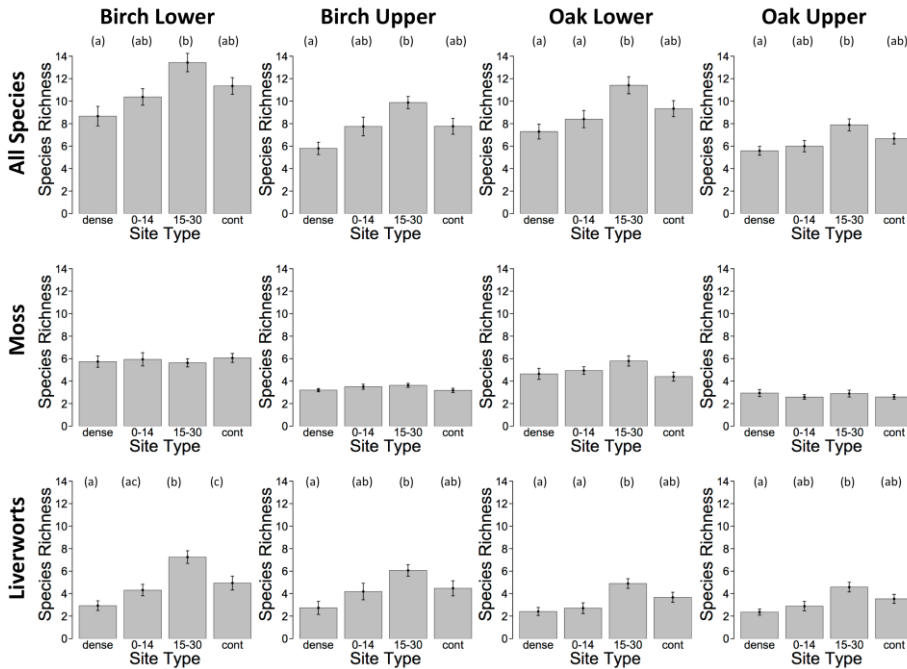711 communities in central America. *Ecology*, **84**, 948-954.

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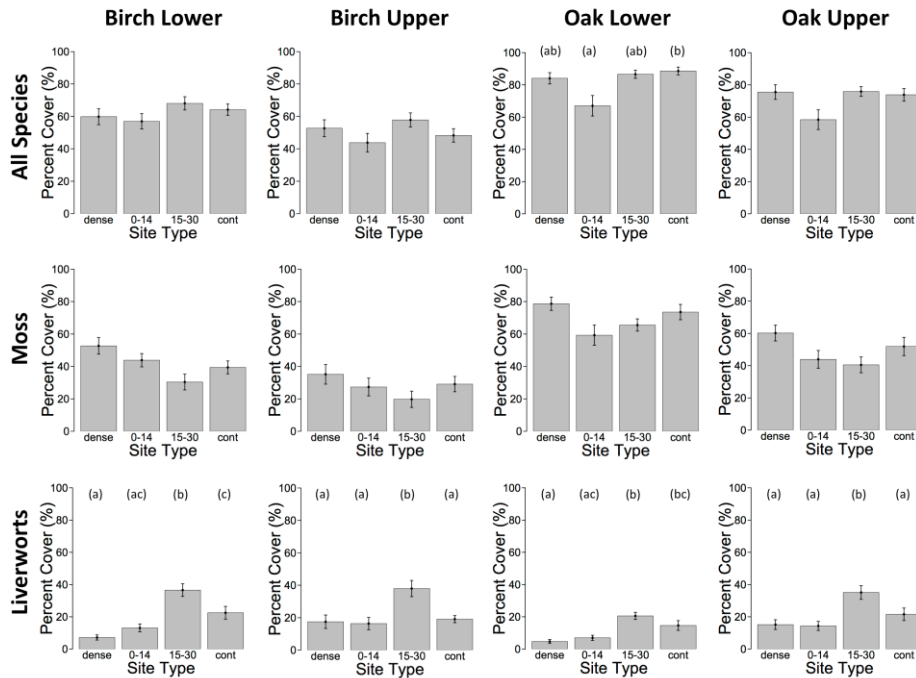
713
714
715 **Fig. 1: The difference in percent cover of all species (row 1), mosses (row**
716 **2), and liverworts (row 3) between different *Rhododendron* site types.** Site
717 types are dense *Rhododendron* (dense), recently cleared sites (0-14 years since
718 clearance), sites that have been clear from *Rhododendron* for a longer period of
719 time (15-30 years since clearance) and uninvaded control plots (cont). Letters
720 above each graph show significant differences (P < 0.05) between site types as
721 revealed by Tukey's HSD test. Graphs with no letters have no significant
722 differences between the site types. Error bars show standard errors.
723

Fig. 2: The difference in species richness of all species (row 1), mosses (row 2), and liverworts (row 3) between different *Rhododendron* site types. Site types are dense *Rhododendron* (dense), recently cleared sites (0-14 years since clearance), sites that have been clear from *Rhododendron* for a longer period of time (15-30 years since clearance) and uninvaded control plots (cont). Letters above each graph show significant differences (P < 0.05) between site types as revealed by Tukey's HSD test. Graphs with no letters have no significant differences between the site types. Error bars show standard errors.
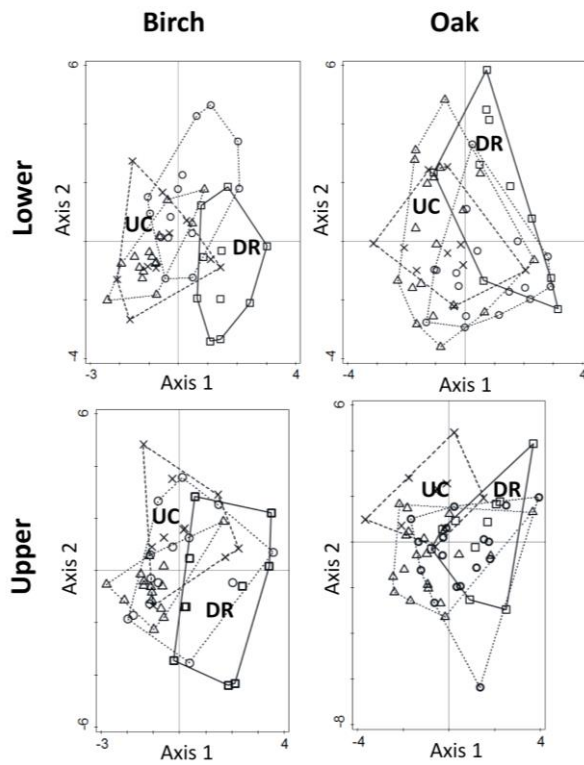
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739
740 **Fig. 3: Differences in community composition between different**
741 ***Rhododendron* sites types.** Classified plot diagrams from the partial-RDA
742 looking at the effect of *Rhododendron* site type on community composition. The
743 shapes delineate the extent of the plots belonging to the same *Rhododendron* site
744 type. Sites with dense *Rhododendron* = DR (□, ——); uninvaded control sites =
745 UC (×, ----); plots cleared 1-14 years ago = (○, ⋯⋯); plots cleared 15-30 years ago
746 = (Δ, ⋯⋯).
747
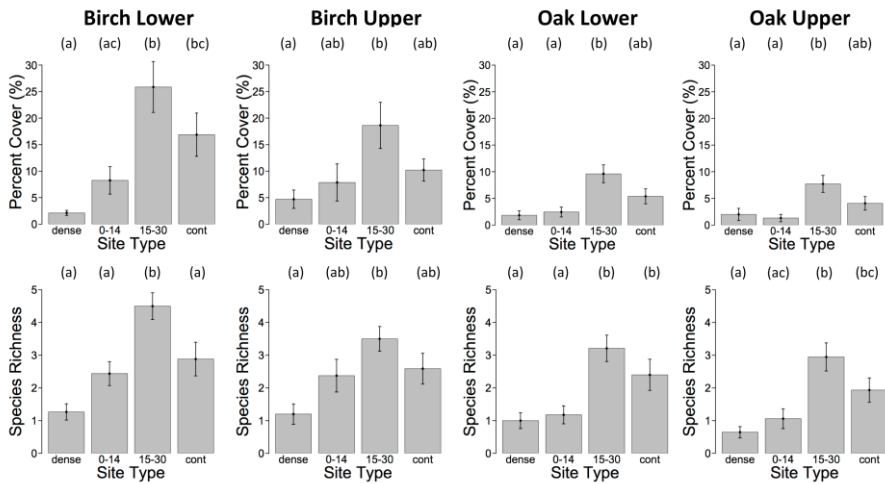
Fig. 4: The difference in percent cover (row 1) and species richness (row 2) for Atlantic species in the different *Rhododendron* site types. Site types are dense *Rhododendron* (dense), recently cleared sites (0-14 years since clearance), sites that have been clear from *Rhododendron* for a longer period of time (15-30 years since clearance) and uninvaded control plots (cont). Letters above each graph show significant differences (P < 0.05) between site types as revealed by Tukey's HSD test. Error bars show standard errors.
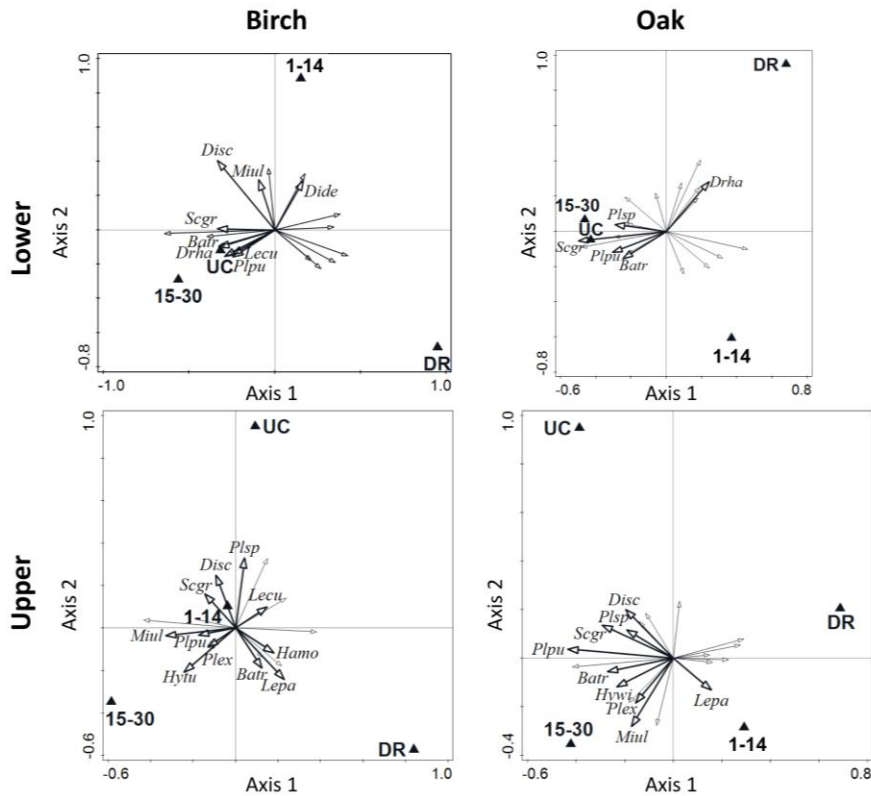
Fig. 5: Response of Atlantic species to *Rhododendron* treatment. The graphs show the results of partial-RDAs revealing the affinity of different atlantic species for plots with dense *Rhododendron* (DR), plots where *Rhododendron* had been cleared 1-14 or 15-30 years previously, and uninvaded control plots (UC). Triangles show the centroid of the scores for plots belonging to that *Rhododendron* site type. Atlantic species only are identified to make the plots clearer (these graphs are presented with all species labelled in the Supporting Information). Atlantic species showed a clear preference for cleared and uninvaded control plots. Species are: ***Batr – *** *Bazzania trilobata;* ***Dide – *** *Dicranodontium denudatum;* ***Disc - *** *Dicranum scottianum;* ***Drha - *** *Drepanolejeunea hamatifolia;* ***Hamo – *** *Harpalejeunea molleri;* ***Hywi – *** *Hymenophyllum wilsonii;* ***Lecu – *** *Lepidozia cupressina;* ***Lepa – *** *Lejeunea patens;* ***Miul – *** *Microlejeunea ulcina;* ***Plex – *** *Plagiochila exigua;* ***Plpu – *** *Plagiochila punctata;* ***Plsp – *** *Plagiochila spinulosa;* ***Scgr – *** *Scapania gracilis.*