How does grazing management influence the functional diversity of oak woodland ecosystems? A plant trait approach.

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2 woodland ecosystems? A plant trait approach.

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Abstract

8 Traditional approaches to conservation often focus on plant species composition. In contrast,

9 trait-based approaches highlight the role plant species play in ecosystem function, with a

10 focus on functional diversity and its importance for ecosystem resilience. Here we utilise a

11 plant-trait approach to explore the association between livestock grazing intensity and plant

12 functional diversity in Atlantic oak woodlands, a conservation priority habitat. In two

13 historically un-grazed woodlands (subject to periods of light sheep grazing in winter) paired

14 with two grazed woodlands (intensively grazed by sheep or feral goats), in north-west Wales,

15 UK, field plant-trait data were recorded in three (30 x 4 m) plots per woodland for trees,

16 saplings and understory plants. For trees and saplings, plant-trait data from the field (specific

17 leaf area (SLA) and leaf dry matter content (LDMC)) were combined with plant tolerance

18 indices from the scientific literature (shade, drought and water-logging tolerance) and used

19 to calculate community weighted means (CWM) and functional diversity for plot-level

20 communities. Three plant traits (LDMC, mean foliage height and growth form) and two

21 Ellenberg indices (light and moisture) were combined to calculate CWM and functional

22 diversity for understory plant communities. Tree and sapling communities from grazed

23 woodlands were characterised by response traits associated with grazing avoidance

24 strategies (high LDMC, low SLA), and higher shade- and drought-tolerance scores but lower

25 water-logging-tolerance scores than in un-grazed woodlands. Tree and sapling communities

26 in the un-grazed woodlands had greater seedling establishment, sapling recruitment and

27 functional diversity than in the grazed woodlands. Plant-trait values and functional diversity

28 did not differ with grazing intensity for understory plants. Land managers are increasingly

29 being asked to manage semi-natural habitats for 'resilience to future events' such as droughts

30 or floods. Here we demonstrate how a plant-trait approach, including assessment of

31 community-level tolerance indices, allows us to infer potential associations between grazing

32 management, functional diversity and ecosystem resilience.

36

37 **1. Introduction**

38 Atlantic oak woodlands are a priority ecosystem for conservation within Europe (European

39 Commission, 2015), characterised by high rainfall, base-poor soils and biodiverse bryophyte

40 communities. Despite their high conservation importance many are listed as having

41 unfavourable conservation status, threatened by fragmentation, inappropriate grazing

42 management and invasive species (JNCC, 2013). Traditional approaches to woodland

43 conservation focus on plant community composition and diversity (Hansson, 2001; McEvoy

44 et al., 2006) and sapling recruitment (Palmer et al., 2004), with poor regeneration of oak

45 (*Quercus* spp.) of particular concern (Shaw, 1968a; 1968b). More recently, trait-based

46 approaches to plant community ecology have been advocated, as a basis for conservation

47 management, in a range of terrestrial ecosystems (Cadotte, 2011) including forests (Andersen

48 et al., 2012; Craven et al., 2016; Mokany et al., 2015). These trait-based approaches highlight

49 the role plant species play in ecosystem function, exploring the emerging relationship

50 between functional diversity and resilience to future perturbations (Standish et al., 2014).

51 Here we define *resilience* as the degree to which ecosystem function can resist or recover

52 rapidly from environmental perturbations (Oliver et al. 2015) as mediated by plant functional

53 traits.

54 Plant functional traits can be defined in two broad ways: i) as any measurable characteristics

55 at the individual level that directly or indirectly affect plant fitness (Lavorel et al., 1997; Violle

56 et al., 2007); or ii) characteristics of individuals or species that influence ecosystem-level

57 properties and processes (Petchey and Gaston, 2006). Plant traits are commonly categorised

58 as either: i) *response traits* – traits associated with an individual or species response to

59 environmental change such as grazing, drought or flooding; or ii) *effect traits* – traits that

60 determine the effect of plants on ecosystem functions such as nutrient or biogeochemical

61 cycling (Lavorel and Garnier, 2002). A greater functional diversity (i.e. variation in functional

62 traits within a community) of effect traits is expected to result in enhanced community-level

63 plant productivity and resource-use efficiency (Díaz et al., 2001). For response traits, greater

64 functional diversity can enhance a community's resilience to a range of environmental

65 disturbances (Díaz et al., 2001; Elmqvist et al., 2003; Loreau et al., 2001; Standish et al., 2014),

66 such as grazing by large herbivores, flooding or drought, by providing a higher response

67 diversity.

68   The impact of livestock grazing on community-level plant traits has been summarised by

69   several classic plant-resource models: Grime's (1977) CSR (Competitor, Stress-tolerator,

70   Ruderal) model, Coley et al.'s (1985) resource availability model and Westoby's (1998) LHS

71   (leaf-height-seed) model. These models predict that: i) selective or low-intensity grazing

72   favours unpalatable plants with low specific leaf area (SLA) (Cornelissen et al., 1999;

73   Coughenour, 1985) and higher leaf dry matter content (LDMC) (grazing avoidance); and ii)

74   intensive non-selective grazing favours short, often palatable, plants with high SLA indicating

75   fast regrowth of high-quality tissue with low structural defence (grazing tolerance),

76   particularly in humid or productive grassland systems (Díaz et al., 2001). This framework,

77   particularly relevant in woodlands to understory plant species, may also be affected by

78   canopy openness with more open woodlands characterised by fast-growing understory

79   species with traits indicative of grazing tolerance strategies such as high SLA (Brocque et al.,

80   2009). For sapling communities, grazing avoidance strategies may be favoured, with low SLA

81   and high LDMC effective at deterring herbivory (Westoby et al. 2002) as these traits tend to

82   be coupled with the allocation of more tannins, phenols or other defensive compounds to

83   leaves (Coley, 1983). Indeed, under open-canopy and intensive livestock-grazing conditions,

84   sapling SLA was found to be lower than in un-grazed forests (Carlucci et al., 2012).

85   In addition to commonly studied response traits such as SLA and LDMC, traits linked to plant

86   response to variation in the physical environment, e.g. tolerance of shade, drought and water-

87   logging, have recently been incorporated into studies evaluating the impact of land-use

88   intensity on functional diversity and ecosystem resilience (Carreño-Rocabado et al., 2012;

89   Carreño-Rocabado et al., 2016; Craven et al., 2016). Some studies have focused on how

90   grazing interacts with response plant-traits related to the physical environment, especially

91   drought tolerance (Deléglise et al., 2015, Leiva et al., 2013; Plieninger et al., 2011; Tucker et

4

92 al., 2011). In a further advance, Niinemets and Valladares (2006) developed proxies for

93 environmental response plant-traits based primarily on Ellenberg indices of shade, drought

94 and water-logging tolerance which they extrapolated to over 800 species of trees and shrubs

95 from the northern hemisphere, in lieu of trait-specific information.

96 The effect of grazing on plant functional diversity has been discussed through the lens of

97 'environmental filtering' where strong abiotic or biotic filtering effects (e.g. heavy grazing

98 pressure) are expected to select for convergent trait values for co-occurring species, leading

99 to a loss of functional diversity (Ackerly and Cornwell, 2007; Cavendar-Bares et al., 2004; Kraft

100 et al., 2008). Most studies on the impact of livestock grazing on functional diversity in

101 woodland ecosystems have focused on the understory plant community, finding that an

102 increase in grazing intensity leads to either increased (Mandle & Ticktin, 2015) or decreased

103 (de Bello et al., 2006) functional diversity. Results from studies of the response of grassland

104 functional diversity to livestock grazing are also inconsistent, with grazing either reducing

105 plant functional diversity by favouring a limited set of trait values related to either avoidance

106 or tolerance strategies (Catorci et al., 2014) or enhancing it, when compared to un-grazed

107 grasslands where tall grasses dominate (Komac et al., 2015; Vandewalle et al., 2014).

108 In this study we utilised a plant-trait approach to explore the association between livestock

109 grazing and plant community response traits, tolerance indices and functional diversity in oak

110 woodlands. We expected: 1) in the understory plant community of grazed woodlands

111 response trait values associated with grazing tolerance strategies (low LDMC, low mean

112 foliage height) to dominate; 2) in the tree and sapling communities of grazed woodlands

113 response traits linked to grazing avoidance strategies (e.g. low SLA, high LDMC) to dominate;

114 3) in the tree and sapling communities of both grazed and un-grazed woodlands trait values

115 associated with shade and water-logging tolerance scores to be greater than those associated

116 with drought tolerance due to the high year-round rainfall in the study area; 4) in the un-

117 grazed woodland plant communities functional diversity to be greater due to the effect of

118 environmental filtering on the grazed woodlands.

119

120 **2. Methods**

121 *2.1 Study area and sampling design*

122 Two pairs of Atlantic oak woodlands, identified as upland oakwood, a priority habitat for

123 conservation and designated as Site(s) of Special Scientific Interest (SSSI), were selected in

124 north-west Wales, UK. One pair is in the area of Ceunant Llennyrch and the other 15 km away

125 in Nant Gwynant (Table 1).These woodlands are managed by the government conservation

126 agency Natural Resources Wales (NRW), alongside two non-governmental organisations: the

127 Woodland Trust (at Ceunant Llennyrch) and the National Trust (at Nant Gwynant). These

128 woodlands are remnants of natural woodland that originally covered most of the Atlantic

129 fringe of Europe, influenced by the Gulf Stream to create the warm, wet microclimate of a

130 temperate rainforest with > 200 days per year of precipitation ≥ 1 mm (JNCC, 2013). Annual

131 precipitation is ~3400 mm with mean, maximum and minimum temperatures of ~10, 19 and

132 -1.5 C respectively (Robinson et al. 2017). These woodlands are dominated by *Quercus*

133 *petraea*, with lower abundance of *Betula pubescens*, *Corylus avellana*, *Fraxinus excelsior*,

134 *Sorbus aucuparia* and *Ilex aquifolium*. Within each of the two study areas, one woodland was

135 selected that had a known history of intensive grazing (managed sheep or feral goat) for at

136 least the past 25 years, and the other managed with no or only light winter grazing over the

137 same time period due to fencing to exclude the animals (Table 1). Sheep and feral goats were

138   the only large mammal herbivores in the study area over this period with cattle and deer

139   absent [Local Environmental Records Centres Wales, http://www.lercwales.org.uk/]. For

140   Ceunant Llennyrch the paired woodlands were adjacent to each other, with the intensively

141   grazed woodland close to sheep grazed pasture-grassland. For Nant Gwynant the selected

142   woodlands were on opposite sides of the valley, 1 km apart, separated by a road and a lake

143   (Llyn Dinas) but both of similar elevation and adjacent to heathland habitat. Soils were

144   classified for both sets of paired woodlands as freely draining acid loamy soils on rock using

145   Soilscapes, a 1:250,000-scale, simplified soils map covering England and Wales developed by

146   the LandIS [Land Information System) team, Cranfield University, http://www.landis.org.uk/].

147   After a preliminary survey to assess the conditions typical of each woodland (i.e. species

148   composition and relative abundance of trees, saplings and understory plants, and slope

149   angle), three 30 m x 4 m plots were established within each of the four study woodlands to

150   represent these conditions. Plots were positioned ≥ 10 m away from woodland edges with

151   large rocky outcrops excluded. All plots included *Q. petraea* and other tree species

152   representative of each woodland. In addition, three 1 m x 1 m sub-plots were established,

153   equally spaced along the length of each plot, for assessment of environmental and understory

154   characteristics including seedling establishment (Appendix, Fig. A1).

155   *2.2 Environmental characterisation*

156   Total basal area (m^2 ha^{-1}) and stems per hectare (ha^{-1}) of trees and saplings were calculated

157   from the mean of plot-level measurements and scaled up. Seedling density (m^{-2}) was

158   calculated from 1 m x 1 m sub-plots. Soil temperature, moisture, pH and bulk density were

159   recorded in each sub-plot. Soil temperature was measured across the top 10 cm of soil with

160   a Checktemp thermometer (Hanna Instruments). Soil pH was measured in water according to

161 Smith and Doran (1996) in a 1:2.5 v/v slurry. Soil bulk density in the top 5 cm of soil was

162 measured using a stainless steel ring (5 cm height, 5 cm diameter). Gravimetric soil moisture

163 content (%) was also calculated from each bulk density soil sample. All environmental

164 characteristics were measured during July 2016; on four days within a 14 day window,

165 avoiding days with precipitation ≥ 3 mm.

166 *2.3 Plants traits*

167 All plant trait data were collected in July 2016, in tandem with the environmental sampling.

168 Within each plot all trees (≥ 10 cm diameter at breast height (1.3 m, DBH) and saplings (<10

169 cm DBH but > 1.3 m height) were identified to species level, with DBH and height (of saplings)

170 recorded. Relative abundance of each species was assessed for trees and saplings combined,

171 based on relative density (stems per hectare), with leaf traits assessed for the species

172 collectively contributing to ≥90 % of total woody plant density, as in de la Riva et al. (2016).

173 Within each sub-plot percentage cover of each understory plant species (including

174 bryophytes) was assessed by eye, tree seedling density recorded and mean foliage height of

175 each species of plant also measured. Epiphytes were not recorded. Leaf traits were also

176 assessed for understory species contributing to approximately ≥90 % of woodland understory

177 cover and were sampled at the main plot level.

178 For each species of tree or sapling selected for leaf trait assessment, three individuals were

179 selected for sampling in each plot. For each individual, three leaves were selected on the basis

180 of: i) height of leaves on trees, all leaves were located on branches accessible from the ground

181 ~1-2 m high; ii) excluding leaves with obvious signs of vertebrate or invertebrate herbivore

182 damage, pathogen damage or necrosis; iii) outer canopy leaves were collected, either sun

183 exposed or least shaded dependant on plot canopy openness (for woodland stand

184 characteristics see Table 2). For each understory species selected for leaf trait assessment

185 three individuals were selected for sampling in each plot. For each individual, three leaves

186 were selected on the basis of: i) foliage height of leaves, with leaves selected from the

187 uppermost foliage in the least shaded part of the plot; ii) avoiding leaf damage as stated above

188 for trees and saplings; iii) for plants with very small or rolled leaves more than three leaves

189 were collected; iv) for bryophytes the top 2 cm of each gametophyte (stem and leaflets) was

190 used as a leaf substitute.

191 Leaves selected for plant trait assessment were collected (while still attached to a length of

192 stem of ~ 2 cm) for trees, saplings and understory plants, wrapped in moist paper and sealed

193 in plastic bags (to avoid dehydration and maximise humidity during temporary storage) as in

194 Perez-Harguindeguy et al. (2013) and placed in a cool box (~ 10 °C). Leaf traits were assessed

195 within 24 hours of leaf collection. Prior to measurement of leaf traits each leaf (including

196 petiole) was cut from its stem and patted dry. One-sided projected leaf area was measured

197 using a Portable Area Meter (LI-3000A, LI-COR) attached to a Belt Conveyer (LI-3050A, LI-

198 COR). Fresh mass and oven-dry mass (60 °C for 72 hours) of each leaf were measured with a

199 4-figure balance. Specific leaf area was calculated by dividing the one-sided area of a fresh

200 leaf by its oven-dry mass (m^2 kg^{-1} or mm^2 mg^{-1}). Leaf dry matter content was calculated by

201 dividing the oven-dry mass (mg) of a leaf by its water-saturated fresh mass (g), expressed as

202 mg g^{-1}. For *Calluna vulgaris*, *Festuca rubra* and bryophyte species projected leaf area was not

203 measured due to their non-flat leaf surface but LDMC was recorded. Each understory plant

204 was allocated one of five growth forms: bryophyte, fern, forb, graminoid (grass, rush and

205 sedge) and shrub.

206 *2.4 Plant tolerance indices*

207   Shade, drought and water-logging tolerance scores [0 (no tolerance) to 5 (maximal tolerance)]

208   were assigned to tree species using indices developed for European tree species (Niinemets

209   and Valladares, 2006). Shade tolerance indices were largely derived from the Ellenberg

210   indicator for light, drought tolerance indices were based primarily on the inverse of Ellenberg

211   indicator values for moisture and water-logging tolerance (i.e. tolerance of reduced root-zone

212   soil oxygen availability) were based on multiple studies. Ellenberg indicator scores for light [1

213   (plant in deep shade) to 9 (plant in full light/sun)] and moisture [1 (indicator of extreme

214   dryness) to 9 (submerged plant)] were allocated to understory plants using updated UK values

215   (Hill et al., 1999; Hill et al., 2000) as in Smart et al. (2010) and Kimberley et al. (2014).

216   *2.5 Statistical analyses*

217   All analysis was carried out in R (R core team, 2016). To assess the association between grazing

218   management (grazed *versus* un-grazed) and environmental variables (e.g. soil temperature)

219   linear mixed-effect models were used with plot nested within location to avoid pseudo-

220   replication (i.e. 'random = ~1|Location/Plot'). 'Woodland' is not included as part of the

221   random effect as each pair of woodlands within each location constituted one grazed and one

222   un-grazed woodland, therefore this is accounted for in the grazing effect.

223   Community-level weighted means (CWM) of trait values were calculated for a set of

224   communities (i.e. plots, n = 3 for each woodland) for: i) trees and saplings combined; ii) trees

225   only; iii) saplings only; and iv) understory plants. For trees and saplings (i, ii and iii) CWM were

226   calculated for 2 plant traits (SLA, LDMC) and 3 tolerance indices (shade, drought and water-

227   logging). For understory plants (iv) CWM were calculated for 3 plant traits (LDMC, mean

228   foliage height, growth form) and 2 Ellenberg indices (light and moisture). For a numeric trait

229   (e.g. SLA), CWM is the mean trait value of all species present in the community (plot),

weighted by their relative abundances (i.e. stem density per plot for trees and saplings, % cover for understory plants), calculated from a species-by-trait(s) matrix. For categorical traits (e.g. growth form), the dominant class is returned as the result (e.g. graminoid or bryophyte). Mean trait values of plant species were used for the calculation of CWM for understory plants (iv) in this study. However, as trees and saplings of the same species (e.g. *Q. petraea*) were often dimorphic (open grown trees *versus* understory saplings), and differed in mean values of plant traits measured in the field (SLA, LDMC) they were considered as separate 'species' for the purpose of calculating CWM for (i) trees and saplings combined. The mean trait (SLA and LDMC) value for each species of tree (ii) or sapling (iii) was used in the species-by-traits matrix. Trees and saplings of the same species were allocated the same score for tolerance indices in the species-by-traits matrix. CWM were calculated using the FD package (Laliberté et al., 2014). Separate CWM values for each of the three plots per woodland were used in a further analysis to assess the association between grazing management and tree, sapling and understory plant traits utilising linear mixed-effects models, nested as described above.

Functional diversity of each woodland community was calculated at the plot level (n = 3 per woodland) for trees and saplings for 2 plant traits (SLA, LDMC) and 3 tolerance indices (shade, drought and water-logging combined). For understory plants, functional diversity was calculated for 3 plant traits (LDMC, mean foliage height, growth form) and 2 Ellenberg indices (light and moisture) combined. Functional diversity was calculated, from the same species-by-traits matrices used in the CWM analysis, using principal coordinates analysis (PCoA) to return PCoA axes, which were then used as 'traits' to compute functional diversity indices, specifically functional dispersion, of each plot using the FD package. Functional dispersion was defined as the mean distance in multi-dimensional trait space of individual species to the centroid of all species, weighted by abundance (Laliberté and Legendre, 2010). For model (i),

254   trees and saplings combined, trees and saplings of the same species were again considered

255   as separate 'species' for the calculation of functional diversity. Functional dispersion was an

256   appropriate index to use in this study as: (a) it is unaffected by species richness, therefore

257   allowing the different trait values of species measured on three individual trees or saplings

258   per plot to be entered into the analysis as different 'species' without artificially inflating the

259   diversity index; (b) it can be computed when traits outnumber species, as occurred for some

260   plots and; (c) it requires only two species to compute functional diversity. In contrast, the

261   suite of three commonly used functional diversity measures, functional richness, evenness

262   and divergence need a minimum of three species per community to be computed.

263

264   **3. Results**

265   *3.1 Environmental and plant community characterisation*

266   The two grazed woodlands were characterised by greater basal area and tree density (total

267   basal area of trees and saplings, and number of tree stems per hectare) than the two un-

268   grazed woodlands, with sapling and tree seedling density greater in the un-grazed woods

269   (Table 2). Diameter size-class distributions showed a greater dominance of the combined tree

270   and sapling populations by the smaller size classes in the two un-grazed than the two grazed

271   woodlands (Appendix, Fig. A2). The two grazed woodlands were dominated by *Q. petraea*

272   trees with some *C. avellana* and *F. excelsior,* while the two un-grazed woodlands were co-

273   dominated by *Q. petraea* and *B. pubescens* trees with saplings of these two species, *S.*

274   *aucuparia* and *I. aquifolium* (Appendix, Fig. A3). Bryophytes, such as *Thuidium tamariscinum*,

275   and the fern *Pteridium aquilinum* occurred in all four woodlands, with graminoids more

276   prevalent in the grazed than the un-grazed woodlands, with cover varying in magnitude with

277 location. Understory shrubs such as *C. vulgaris*, *Vaccinium myrtillus* and *Rubus fruticosus* were

278 only found in un-grazed woodlands (Appendix, Fig. A4). Soil temperature and pH were greater

279 in the grazed than un-grazed woodlands with soil moisture content greater in the un-grazed

280 woodlands (Table 2). Soil bulk density did not differ significantly with grazing.

281 *3.2 CWM of plant traits and tolerance indices*

282 Tree and sapling communities in the main plots had significantly greater LDMC in the grazed

283 than the un-grazed woodlands, with SLA significantly lower in the grazed woodlands (Table

284 3). Tree and sapling communities had significantly higher shade- and drought-tolerance

285 scores but lower water-logging-tolerance scores in the grazed than un-grazed woodlands. The

286 relationship between grazing and LDMC in the woodland plots appeared to be linked primarily

287 to saplings, with differences in the tolerance indices associated mainly with trees (Table 3). In

288 contrast, understory plant trait values did not differ significantly between the grazed and un-

289 grazed woodlands (Table 4). Mean SLA and LDMC of tree, sapling and understory plant species

290 are shown in the Appendix (Fig. A5-A6).

291 *3.3 Functional diversity*

292 Tree and sapling communities had significantly greater functional diversity in the un-grazed

293 than grazed woodlands ($P < 0.01$, Table 5). Understory plant functional diversity did not differ

294 significantly with grazing.

295

296 **4. Discussion**

297 *4.1 Understory community: response-traits*

298   In this study, the understory community did not exhibit clear differences in field-measured

299   plant response traits (LDMC, mean foliage height and growth form) between the grazed and

300   un-grazed Atlantic oak woodlands. We can therefore reject our first hypothesis, based on

301   classic plant-resource models (Coley et al., 1985; Grime, 1977; Westoby, 1998), that response

302   traits associated with grazing tolerance strategies (low LDMC and low mean foliage height)

303   will dominate in grazed understory plant communities. Despite this, there are differences

304   apparent between the woodlands that have not been adequately captured by the plant-trait

305   approach. Whilst bryophytes (high LDMC) occurred in both the grazed and un-grazed study

306   woodlands, the woody shrubs *C. vulgaris*, *V. myrtillus* and *R. fruticosus* (with medium -LDMC

307   values) were only found in the un-grazed woodlands. The understory vegetation of the

308   intensively sheep-grazed woodland was characterised by bryophytes and a mixture of fine

309   (e.g. *F. rubra*) and coarse (e.g. *Deschampsia flexuosa*) grasses (with variable SLA). However,

310   the understory of the feral goat-grazed woodland was dominated by the unpalatable tall

311   tussocky grass species, *Molinia caerulea* (high LDMC). In summary, the understory vegetation

312   of the grazed woodlands was dominated by species exhibiting either grazing tolerance (e.g.

313   small stature, high SLA, low LDMC) or grazing avoidance (e.g. low SLA, high LDMC) strategies,

314   sometimes in combination. A caveat of the plant-trait approach is that community-level plant

315   response trait means for each woodland do not accurately represent these compensatory

316   responses to grazing pressure, especially where antagonistic and synergistic responses cancel

317   each other out.

318   *4.2 Tree and sapling community: response-traits*

319   Whilst the understory plant community is subject to direct contemporary grazing effects, tree

320   and sapling communities are more reflective of the longer-term direct and indirect effects of

321   grazing on their recruitment and earlier performance. We therefore consider the plant-trait

322   response to grazing of the tree and sapling community separately to the understory

323   community. For the two grazed woodlands in this study, results conformed to the prediction

324   that response traits linked to grazing-avoidance strategies (low SLA and high LDMC) dominate

325   in tree and sapling communities. These results are in line with the findings of Carlucci et al.

326   (2012) but not the grazing tolerance-avoidance frameworks of classic plant-resource models

327   (Coley et al., 1985; Grime, 1977; Westoby, 1998). Whilst potentially useful for characterising

328   plant-response-traits in woodland understory plant communities, these models are not

329   supported by the results of our study, which we suggest indicates that they are not as useful

330   for defining grazing tolerance-avoidance strategies for perennial plants such as trees where

331   true tolerance is rare. Indeed, evidence for grazing-tolerance in woodland ecosystems is

332   sparse and tends to focus on arid woodlands (Meers et al., 2008; Vesk et al., 2004).

333   An alternative explanation to grazing avoidance or tolerance strategies driving the species

334   composition of grazed woodland communities, is that un-grazed tree and sapling

335   communities contain pioneer trees such as *B. pubescens* as a result of reduced competition,

336   due to the relative lack of mature trees in comparison to the grazed woodlands. These grazing

337   intolerant species exhibit a more 'acquisitive', rapid growth strategy (high SLA, low LDMC)

338   than the species dominant in grazed woodlands, such as *Q. petraea* with a more 'conservative'

339   slow-growth strategy (Díaz et al., 2004). In addition, the two field-measured plant traits (SLA

340   and LDMC) are both leaf traits and do not take into account the variation between tree

341   species in palatability of their bark to grazing livestock, which is important for sapling

342   recruitment. There is evidence that livestock tend to strip the bark of more palatable species,

343   e.g. *Acer pseudoplatanus* and *Castanea sativa*, whereas the bark of others such as *Q. petraea*

344   is more impenetrable to livestock teeth when older (Mayle, 1999). Despite differing in feeding

345 strategies, both sheep (primarily grazers) and goats (browsers) feed on both whole saplings

346 and tree leaves within reach, particularly when other good quality forage is limited (Pollock

347 et al., 2005). High intensity browsing can reduce growth rates of saplings resulting in trees

348 with a short, wide dwarfed stature and highly branched canopies (Kinnaird, 1974).

349 *4.3 Tree and sapling community: plant tolerance indices*

350 We predicted that shade- and water-logging-tolerance scores would be greater than drought-

351 tolerance scores for both grazed and un-grazed woodlands, due to the high rainfall in the

352 study area. However, results showed that this was not the case, with large differences in

353 scores between the grazed and un-grazed woodlands. Water-logging tolerance scores were

354 greater in the un-grazed than grazed tree and sapling communities reflecting, in part, the low

355 water-logging tolerance score attributed to *Q. petraea* (1.2), dominant in grazed sites, and

356 high score for *B. pubescens* (2.98), found only in un-grazed woodlands. In contrast, drought

357 and shade tolerance scores were greater in grazed woodlands. The characterisation of the

358 grazed woodlands as drought-tolerant communities was largely attributable to their greater

359 dominance by *Q. petraea*, which has a relatively high drought tolerance score (3.02)

360 compared with the species that were more abundant in the un-grazed woodlands, e.g. *B.*

361 *pubescens* (1.27) and *S. aucuparia* (2.11). Plant species with traits associated with drought

362 avoidance (e.g. leaf shedding or investment in elaborate deep root systems that can reach

363 the water table all year round) can be amongst the best drought survivors, with evidence from

364 tropical dry forests (Poorter and Markesteijn, 2008). The functional traits that describe such

365 drought tolerance or avoidance strategies are at opposite ends of the 'acquisitive-

366 conservative' trait value continuum, e.g. high LDMC, wood density and low SLA in drought

367 tolerant species, low LDMC, wood density and high SLA in drought avoiders. They would

368   nonetheless have similar Ellenberg values and so would not be distinguished by the indices

369   used in this study.

370   *4.4. Tree and sapling community: Functional diversity and resilience*

371   Whilst uncertainty as to the relative tolerance of individual species to future perturbations

372   such as drought or flooding remains, there is now broad consensus that diversity of species,

373   functional diversity in particular, is key to ecosystem resilience (Standish et al., 2014).

374   Therefore, it is likely that communities such as the un-grazed trees and saplings of the present

375   study, which exhibit a wide range of functional diversity for both tolerance indices (e.g. shade,

376   drought and water-logging) and response-plant-traits (e.g. SLA and LDMC), would be more

377   resilient to future perturbations than the grazed plant communities. In addition, the near

378   complete absence of saplings of any species in grazed woodland communities, indicating the

379   indiscriminate impact of grazing on young plants of tree species, with even seedlings of

380   species exhibiting grazer-avoidance traits unable to survive intensive grazing by either sheep

381   or goats. This lack of recruitment leads to even-aged and species-poor grazed woodland

382   communities, low in functional diversity, with potentially compromised resilience to future

383   disturbances. Of particular relevance to this study are climate-related perturbations, i.e. a

384   projected increase in flood and drought intensity, due to the inherent relationship between

385   functional diversity, as defined here, and certain tolerance indices directly linked to water-

386   logging and drought. It is less clear how grazing intensity and functional diversity would relate

387   to non-climatic disturbances such as fragmentation, or afforestation.

388   *4.5. Intraspecific variation or tree/sapling variation?*

389   Increasingly, plant trait-based approaches are addressing the importance of including

390   intraspecific variation in trait values, as using a single trait value to describe a given species

391 can hide functional variation within species, particularly along environmental gradients

392 (Albert et al., 2010). For the present study both *Q. petraea* and *B. pubescens* saplings exhibited

393 greater SLA and lower LDMC than their trees thus allowing for some of the intraspecific

394 difference in traits to be accounted for by entering saplings and trees of the same species into

395 the CWM analysis with different trait values for field-measured traits. There are several

396 reasons why saplings may differ from trees: i) light levels (for photosynthesising leaves) are

397 likely to be lower for saplings than trees, therefore higher SLA and lower LDMC in saplings

398 may increase their carbon gain under these conditions (Spasojevic et al., 2014); ii) leaves from

399 taller trees experience greater drought stress than saplings, as it is drier high up in the canopy.

400 Thicker cell walls and fibres associated with higher LDMC can be important to maintain leaf

401 turgor under lower leaf water potentials in these drier canopy conditions (Kusar et al., 2009;

402 Zimmerman, 1978); iii) exposure of foliage to both livestock herbivores and small mammals

403 such as voles and rabbits is likely to be greater for seedlings and saplings than for larger trees

404 (Palmer et al., 2004), regardless of their growth or defence response-trait strategies, with

405 seedlings and saplings more likely to suffer grazing-induced mortality; and iv) greater LDMC

406 may provide defence against an accumulated invertebrate herbivore population in older trees

407 (Coley, 1983).

408 *4.6 Oak recruitment and grazing*

409 *Q. petraea* saplings were exclusively found in the un-grazed woodlands, indicating a

410 detrimental effect of grazing animals on recruitment of saplings via seedling grazing, as found

411 by Mountford and Peterken (2003) and Vera (2000), though some limited evidence to the

412 contrary was provided by Annighöfer (2015). Coupled with susceptibility to grazing, *Q.*

413 *petraea* is a light-demanding species that can germinate in the shade but needs open

414 conditions for long-term survival and growth of saplings (Kelly, 2002). In this study *Q. petraea*

415 saplings occurred in semi-open conditions, often close to the thorny shrub *R. fruticosus*,

416 offering the potential of protection from grazing (Kelly, 2002; Vera, 2000). An exclosure

417 experiment, conducted in multiple sites across Europe, found that transplanted *Quercus*

418 *robur* seedlings grew best in grassland exclosures and on the edge of thorny shrub thickets

419 (Bakker et al., 2004), which may be viewed as an optimal balance between sufficient

420 protection from large herbivores and sufficient light availability.

421 **5. Conclusions**

422 Traditional approaches to woodland conservation and grazing management focus primarily

423 on plant community composition, with sapling recruitment and regeneration of oak (*Quercus*

424 spp.) being a particular concern in the British Isles. More recently, trait-based approaches

425 have been advocated as a basis for conservation management, highlighting the role plant

426 species play in ecosystem function and exploring the relationship between functional

427 diversity and resilience to future perturbations such as flooding or drought. Here, we took a

428 primarily trait-based approach, with plant response-traits, tolerance scores (to shade,

429 drought and water-logging) and functional diversity considered (alongside seedling

430 establishment and sapling recruitment) as potential indicators of ecosystem resilience. In this

431 study, woodlands with a recent history of being un-grazed were characterised by greater

432 seedling establishment, sapling recruitment and tree-level functional diversity than their

433 grazed counterparts, indicating a potential association between management to control

434 grazing and ecosystem resilience in Atlantic oak woodlands.

435

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441   **Appendix. Supplementary data**

442   Supplementary data associated with this article can be found, in the online version, at xxxx

443

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643

644   **Table 1** Characteristics of the four study woodlands in north-west Wales, UK.

Location	Ceunant Llennyrch		Nant Gwynant	
Woodland	Llennyrch (L)	Coed Felinrhyd (F)	Hafod y Llan (H)	Llyndy Isaf (I)
Lat/Long (WGS84)	52°55'30.07"N	52°56'06.85"N	53°02'07.49"N	53°01'26.21"N
Elevation (of plots)	~100 m	~ 70 m	~ 70 m	~ 70 m
Grazing category	G	U	G	U
Grazing history	Intensively sheep grazed (80-100 years)	Un-grazed or light sheep grazing in winter only (80-100 years)	Feral goat grazed but sheep excluded (40 years +)	Un-grazed or light sheep grazing in winter only (25 years +)
Condition	Unfavourable	Favourable	Unfavourable	Favourable

645   Condition was reported according to Common Standards Monitoring (CSM) criteria set by the Joint Nature
646   Conservation Committee (JNCC) for Ceunant Llennyrch (Woodland Trust, 2016) and Nant Gwynant (Allen and
647   Brash, 2012; Hearn, 2004; Nouvet et al., 2000). Information on grazing history was also obtained from these
648   references.

649

650 **Table 2** Association of grazing with environmental characteristics of four study woodlands

651 (L, F, H, I) in two locations. Tree (T), sapling (S) and tree seedling summary information are

652 shown for each woodland. Soil variable means are presented for each woodland (n = 3) ±

653 standard error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Grazing
Trees and saplings					
Total basal area (m^2 ha^{-1})	263	138	293	162	↑
T: Stems per hectare (ha^{-1})	1111	889	667	472	↑
S: Stems per hectare (ha^{-1})	0	528	83	1639	↓
Tree seedlings					
Individuals m^{-2}	0.4	1.0	0.1	0.8	↓
Soil					
Temperature (°C)	16.0 ± 0.23	13.6 ± 0.14	14.7 ± 0.10	14.6 ± 0.09	↑ *
Moisture (%)	60 ± 4.20	76 ± 4.70	69 ± 2.97	76 ± 4.20	↓ *
pH (H$_2$0)	4.4 ± 0.07	4.2 ± 0.04	4.4 ± 0.08	4.2 ± 0.04	↑ *
Bulk density (g cm^{-3})	0.26 ± 0.05	0.17 ± 0.05	0.20 ± 0.04	0.13 ± 0.03	*ns*

654 G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing

655 ↑ = larger value, ↓ = smaller value, for G than U woodlands

656 * = *P* < 0.05, *ns* = non-significant

657

Table 3. Association of grazing with tree and sapling community weighted means (CWM) of 2

659   plant response traits (SLA, LDMC) and 3 plant tolerance indices (shade, drought and water-

660   logging) for four study woodlands (L, F, H, I) from two locations. CWM are presented for trees

661   and saplings combined and separately. Means for each woodland (based on n = 3) ± standard

662   error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Association with grazing
SLA					
Trees and saplings	16.6 ± 1.60	18.4 ±1.04	17.0 ± 1.15	21.2 ± 0.96	↓ *
Trees only	16.6 ± 1.60	16.7 ± 0.50	16.2 ± 1.17	16.9 ± 0.74	*ns*
Saplings only	-	21.7 ± 0.15	23.8 ± 0.0	24.4 ± 0.92	*ns*
LDMC					
Trees and saplings	400 ± 9.8	364 ± 13.5	411 ± 0.6	346 ± 5.1	↑ ***
Trees only	400 ± 9.8	379 ± 9.4	411 ± 0.6	374 ± 13.9	↑ *
Saplings only	-	335 ± 1.7	414 ± 0.0	329 ± 4.2	↑ ***
Shade tolerance					
Trees and saplings	2.77 ± 0.04	2.30 ± 0.10	2.91 ± 0.10	2.65 ± 0.22	↑ *
Trees only	2.77 ± 0.04	2.27 ± 0.14	2.84 ± 0.11	2.20 ± 0.20	↑ **
Saplings only	-	2.14 ± 0.17	3.53 ± 0.00	2.86 ± 0.30	*ns*
Drought tolerance					
Trees and saplings	2.99 ± 0.03	2.00 ± 0.25	3.02 ± 0.00	2.20 ± 0.25	↑ ***
Trees only	2.99 ± 0.03	2.10 ± 0.27	3.02 ± 0.00	1.97 ± 0.40	↑ **
Saplings only	-	1.56 ± 0.15	3.04 ± 0.00	2.25 ± 0.21	↑ *
Water-logging tolerance					
Trees and saplings	1.32 ± 0.12	2.25 ± 0.26	1.31 ± 0.06	1.92 ± 0.22	↓ **
Trees only	1.32 ± 0.12	2.13 ± 0.28	1.26 ± 0.06	2.27 ± 0.41	↓ **
Saplings only	-	2.72 ± 0.14	1.68 ± 0.00	1.82 ± 0.19	*ns*

663   G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing
664   SLA = Specific leaf area, LDMC = Leaf dry matter content
665   ↑ = larger value, ↓ = smaller value, for G than U woodlands
666   *** = *P* < 0.001, ** = *P* < 0.01, * = *P* < 0.05, *ns* = non-significant
667

668 **Table 4**. Association of grazing with understory plant community weighted means (CWM) of

669 3 response traits (LDMC, mean foliage height, growth form) and 2 Ellenberg indices (light

670 and moisture) for four study woodlands (L, F, H, I) from two locations. Dominant growth

671 form is a categorical variable so is shown for each woodland at the plot level. Means for

672 each woodland (based on n = 3) ± standard error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Association with grazing
LDMC	336 ± 26.3	337 ± 11.4	314 ± 18.4	340 ± 7.6	*ns*
Mean foliage height	17.4 ± 6.7	26.6 ± 7.6	34.2 ± 0.8	27.3 ± 2.9	*ns*
Light Ellenberg ind.	5.7 ± 0.12	5.6 ± 0.18	6.2 ± 0.09	6.2 ± 0.16	*ns*
Moisture Ellenberg ind.	5.8 ± 0.15	5.9 ± 0.19	6.5 ± 0.28	6.1 ± 0.46	*ns*
Growth form	Bry/Bry/Fer	Shr/Bry/Fer	Gra/Gra/Gra	Bry/Bry/Gra	-

673 G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing
674 LDMC = Leaf dry matter content, Bry = bryophyte, Fer = fern, Shr = shrub, Gra = graminoid
675 *ns* = non-significant
676

677 **Table 5**. Association of grazing intensity with functional diversity (functional dispersion), for

678 trees and saplings based on 2 response traits (SLA, LDMC) and 3 tolerance indices (shade,

679 drought and water-logging) and for understory plants based on 3 response traits (LDMC,

680 mean foliage height, growth form) and 2 Ellenberg indices (light and moisture) for four

681 woodlands (L, F, H, I) from two locations. Means for each woodland (based on n = 3) ±

682 standard error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Association with grazing
Trees and saplings	0.07 ± 0.07	0.26 ± 0.02	0.07 ± 0.04	0.22 ± 0.04	↓ **
Trees only	0.43 ± 0.43	1.35 ± 0.14	0.28 ± 0.28	0.90 ± 0.28	↓ *
Saplings only	-	0.18 ± 0.09	0.00 ± 0.00	0.16 ± 0.06	↓ **
Understory	0.28 ± 0.02	0.24 ± 0.02	0.28 ± 0.02	0.30 ± 0.00	*ns*

683 G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing

684 ↓ = smaller value for grazed than un-grazed.

685 ** = $P < 0.01$, * = $P < 0.05$, *ns* = non-significant

686

687