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1   **Impacts of forestry planting on primary production in upland lakes from north-west**

2   **Ireland**

3   Running head: Algal communities in forested lakes, Ireland

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29   **Abstract**

30   Planted forests are increasing in many upland regions world-wide, but knowledge about their

31   potential effects on algal communities of catchment lakes is relatively unknown. Here the

32   effects of afforestation were investigated using palaeolimnology at six upland lake sites in the

33   north-west of Ireland subject to different extents of forest plantation cover (4-64% of

34   catchment area). ^{210}Pb dated sediment cores were analysed for carotenoid pigments from

35   algae, stable isotopes of bulk carbon (δ^{13}C) and nitrogen (δ^{15}N), and C/N ratios. In lakes

36   with >50% of their catchment area covered by plantations, there were two- to six-fold

37   increases in pigments from cryptophytes (alloxanthin) and significant but lower increases

38   (39-116%) in those from colonial cyanobacteria (canthaxanthin), but no response from

39   biomarkers of total algal abundance (β-carotene). In contrast, lakes in catchments with <20%

40   afforestation exhibited no consistent response to forestry practices, although all lakes

41   exhibited fluctuations in pigments and geochemical variables due to peat cutting and upland

42   grazing prior to forest plantation. Taken together, patterns suggest that increases in

43   cyanobacteria and cryptophyte abundance reflect a combination of mineral and nutrient

44   enrichment associated with forest fertilisation and organic matter influx which may have

45   facilitated growth of mixotrophic taxa. This study demonstrates that planted forests can alter

46   the abundance and community structure of algae in upland humic lakes of Ireland and

47   Northern Ireland, despite long histories of prior catchment disturbance.

Introduction

Planted forests have increased substantially over the past four decades world-wide, with total planted forest area as classified by the United Nations (UN) increasing from 167.5 million hectares in 1990 to 277.9 million hectares in 2015, which accounts for 4.06% to 6.95% of total forest area (Payn *et al.*, 2015). The island of Ireland, although one of the least forested in Europe, has seen plantation forests increase from 2 to 10% of land cover, representing more than 90% of total regional forests (Forest Europe *et al.*, 2011, Department of Agriculture, 2014, Graham *et al.*, 2014). Such forestry can support rural development (McDonagh *et al.*, 2010) and offers an attractive way to sequester greenhouse gases and help offset CO_2 emissions (O'Donnell *et al.*, 2013).

Despite the ecological importance of established forests, afforestation of upland regions through ploughing, planting, fertilisation and felling can potentially impact local water bodies (Foy & Bailey-Watts, 1998, McElarney *et al.*, 2010, Woodward *et al.*, 2012, Drinan *et al.*, 2013b, Drinan *et al.*, 2013a, Dalton *et al.*, 2014, O'Driscoll *et al.*, 2016). While widespread anthropogenic eutrophication of lowland lakes has now been demonstrated across the north temperate-subarctic (Anderson *et al.*, 2014, Taranu *et al.*, 2015), relatively less is known about how afforested lakes in smaller, upland catchments have changed in response to anthropogenic alteration of nutrient cycles. Upland lakes are subjected to multiple stressors which may alter lake ecosystem structure and function both independently and together with forestry practises (Williamson *et al.*, 2009). For example, depopulation migration (e.g., the Great Irish Famine, 1845-1850) can alter land use and lake ecosystem structure as human disturbance declines in the lowland regions (Donohue *et al.*, 2010), and habitation of upland catchments is altered. Similarly, atmospheric deposition of compounds associated with anthropogenic activities can influence upland catchments, including reactive nitrogen (Nr) (Holtgrieve *et al.*, 2011, Wolfe *et al.*, 2013), sulphuric acids, (Catalan *et al.*, 2013),

4

73 phosphorus deposition (Camarero & Catalan, 2012) and pesticides (Rawn *et al.*, 2001).

74 Finally, changes in climate teleconnection patterns such as the North Atlantic Oscillation

75 (NAO) can alter influx of precipitation which in turn influences the input of terrestrial

76 (dissolved organic carbon) DOC to lakes (Monteith *et al.*, 2007). Given this range of

77 potential stressors (Maberly & Elliott, 2012), it is unclear whether upland forest plantations

78 may exert unique measurable effects on algae even though plantation effects are possible.

79   Local disturbance of afforested catchments may include ploughing and planting,

80 which together enhance the release of DOC and POC (particulate organic carbon) into lakes.

81 These influxes may reduce light penetration and limit production (Karlsson *et al.*, 2009).

82 Alternatively, the input of DOC may stimulate mixotrophic algae which obtain energy and

83 nutrition both from phototrophic and phagotrophic heterotrophy (Jones, 2000, Sparber *et al.*,

84 2015). Influx of allochthonous materials from forestry (e.g. eroded silt) may disturb primary

85 production by providing energy to zooplankton and consequent food-web interactions within

86 the lake (Girvan & Foy, 2006). Further, fertilisation of coniferous plantations with

87 phosphorus can cause eutrophication leading to cyanobacterial blooms (Gibson, 1976).

88 Macrophytes may decline over decades due to increased water colour following timber

89 harvest due to soil disturbance and breakdown of brash, releasing DOC in to lakes

90 (McElarney *et al.*, 2010). Additionally, clearcut can cause changes in physical lake mixing,

91 with increased wind access to lake surfaces altering thermal regimes, water column mixing

92 and deep-water oxygen status (Scully *et al.*, 2000). In principle, shifts in treeline position can

93 also influence nitrogen availability in lakes (Bunting *et al.*, 2010), while terrestrial subsidies

94 of allochthonous carbon to lakes can have wide-reaching trophic effects in lentic ecosystems

95 (Cole *et al.*, 2011). However, despite clear effects of forest planting, felling and fertilisation

96 on lake biogeochemistry, little is known of how primary producer communities have been

97   altered in upland lakes. Such effects in landscapes where lakes are abundant, as in Ireland,

98   have the potential to influence regional carbon fluxes (Cole *et al.*, 2007).

99   To explore how forestry plantations might influence upland lake ecology, we

100   compared records of forest planting, felling and extent of forest cover with changes in

101   pigment biomarkers (carotenoids) from algae and cyanobacteria, as well as geochemical

102   proxies of carbon (δ^{13}C) and nitrogen (δ^{15}N) cycling over the past ~150 years in dated

103   sediment cores from six upland lakes spanning a gradient of forestry cover (4-64% of

104   catchment afforested). The main aim was to investigate if planting, felling and percentage

105   forest cover caused significant changes in algal abundance and community composition. We

106   hypothesised that physical and chemical changes caused by high cover of managed forests

107   would overwhelm other local and regional drivers and lead to changes in algal production and

108   community composition. Specifically, we predicted that afforestation would increase algal

109   abundance following forest fertiliser application, or decrease algal abundance due to light

110   limiting DOC. Alternatively, we predicted that increases in DOC could favour mixotrophic

111   taxa (e.g. cryptophytes).

112 **Materials and Methods**

113 *Study area and forestry records*

114 The study region is located in upland moorland areas in the north-west of Ireland across the

115 Republic of Ireland (ROI) and Northern Ireland (NI), which together have a temperate,

116 oceanic climate that has allowed extensive areas of blanket bog to develop (Figure 1).

117 Commercial forest plantations represent the second largest land-use class in the NI region

118 (McElarney *et al.*, 2010) and mostly consist of non-native Sitka spruce (*Picea sitchensis*),

119 Lodgepole pine (*Pinus contorta spp.*) and Norway spruce (*Picea abies*) planted on areas of

120 marginal use for agriculture referred to as rough grazing.
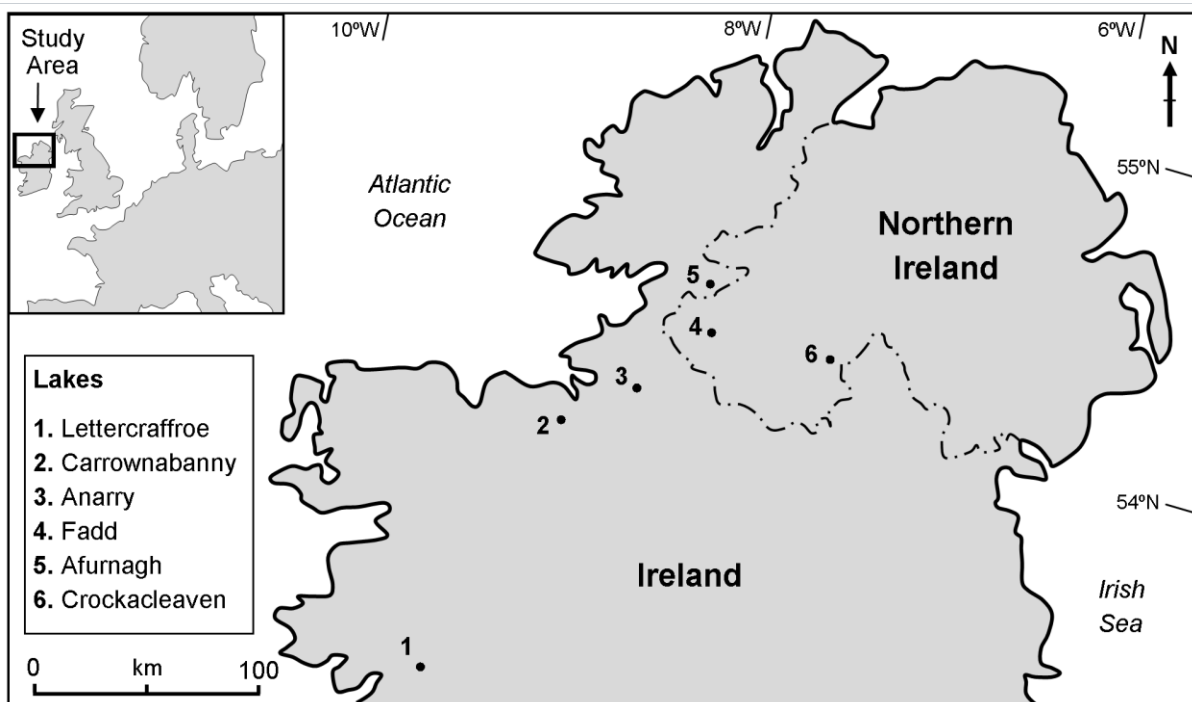
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122 Figure 1: Location of the six study lakes selected for sediment coring.

123

124   Six upland lakes were selected across a gradient of planted maximum forest cover

125   ranging from 4-64% of total catchment area (Tables 1, 2) (Foy & Bailey-Watts, 1998,

126   McElarney *et al.*, 2009, McElarney & Rippey, 2009, McElarney *et al.*, 2010). Lake

127   elevations ranged from 83-183 m a.s.l. (Table 1), while the dominant non forest land-uses

128   were peatland and semi-natural moorland (Table 2). Natural woodland, scrub and an

129   additional small lake was also present in the Fadd catchment, and a small area of pasture was

130   present in Anarry, Carrownabanny and Fadd (Table 2). Generally, the catchments were not

131   populated, with the exception of Carrownabanny and Fadd which have a few rural houses

132   (Table 2). Lake size ranged between 4 and 78 ha, maximum depths varied from 5.5 to 17.9 m;

133   underlying geologies were variable (granite, quartzite, gneiss, schists limestone,

134   shales/sandstone) and catchment soils included peat, humic or gley types (Table 1). Previous

135   water chemistry analyses indicated a range of nutrient conditions (total phosphorus, TP 10.8-

136   65.5 µg L^{-1} and total oxidised nitrogen, TON 0.1-1.1 mgL^{-1}), but all had relatively low

137   phytoplankton biomass (chlorophyll *a* 2.7-9.1 µg L^{-1}), high dissolved organic carbon (DOC)

138   concentrations 8-16.1 mg C L^{-1} and circumneutral pH from 6.3-7.9 (Table 1).

Table 1: Study lakes: location, geology and water chemistry measurements.

	Crockacleaven	Lettercraffroe	Anarry	Carrownabanny	Fadd	Afurnagh
Latitude (N)	54°20'39.20"	53°22'50.56"	54°15'25.44"	54° 9'27.88"	54°25'28.61"	54°33'59.30"
Longitude (W)	7°15'23.53"	9°25'17.39"	8°16'34.79"	8°40'43.84"	7°52'55.63"	7°52'56.97"
Country	NI	ROI	ROI	ROI	NI	ROI
Elevation (m a.s.l)	183	163[a]	83	102	138	123
Lake area (ha)	4	78	12	7.2	6	7
Max depth (m)	5.5	17.9[a]	7.8	6.5	14.5	8.5
Water residence time (years)	0.4	0.6	0.6	0.4	0.4	0.2
Main soil types	Deep peat, humic gley	Rock outcrop, peat	Peat, gley	Gley, peaty gley (grey brown podzols)	Peat, gley	Peat, humic ranker
Bedrock geology	Sandstone, Shales, Limestone	Granite	Pre-Cambiran Quartzite, Gneisses and Schist	Pre-Cambiran Quartzite, Gneisses and Schist. Lake on sandstone.	Sandstone, shales	Pre-Cambiran Quartzite, Gneisses and Schist
Conductivity @20°C (μScm^{-1})	53.9	82.5	85.0	120.3	82.6	66.6
Alkalinity (mequiv l^{-1})	0.1	0.1	0.4	0.6	0.7	0.2
pH	6.3	6.3	6.7	7.4	7.9	7.5
SiO$_2$ (mg l^{-1})	1.6	0.6	1.4	0.3	0.4	1.7
TP (μg l^{-1})	65.5	10.8	37.3	56	11	22.5
TON (mg l^{-1})	1.1	0.2	0.1	0.3	0.5	0.0
Chlorophyll *a* (μg l^{-1})	6.0	9.1	5.0	3.1	3.4	1.4
DOC (mg l^{-1})	14	-	-	16.1	8	11.4

Water chemistry measurements complied from: McElarney *et al.* (2009) and McElarney *et al.* (2010), AFBI sampling and EPA (Ireland) sampling for Water Framework Directive compliance. [a] Denotes lake variables compiled from De Eyto *et al.* (2002). Abbreviations: silica (SiO$_2$), total phosphorus (TP), dissolved organic carbon (DOC), total oxidised nitrogen (TON). For the four lakes in the ROI catchment geology was determined using the Geological Survey of Ireland 1:10000 Bedrock Geology GIS layer while catchment soil types were based on the National Soils Map of Ireland 1:50000 Irish Forest Soils GIS layer (Fealy *et al.*, 2009). For the two lakes in NI the maps of the Northern Ireland Soil Survey (1:50000) and Geological Survey of Northern Ireland (1:63360) were used (Cruickshank, 1997).

Table 2: Study lakes afforestation and land cover compiled from forestry records, historical mapping and aerial imagery.

Lake	Crockacleaven	Lettercraffroe	Anarry	Carrownabanny	Fadd	Afurnagh
First plant (year)	1967 [a]	1960 [b]	1963 [c]	1960 [c]	1996 [c]	1998 [a]
First fell (year)	2000 [a]	2002 [b]	1991 [c]	1991 [c]	-	-
Afforested maximum land cover (%)	64	63	57	19	6	4
Catchment to lake area ratio	4:1	3:1	4:1	7:1	14:1	15:1
Catchment area (excluding lake) (ha)	16	238	53	52	82	102
Heath/moorland/bog (%)	26	37	39	70	76	96
Natural woodland & scrub (%)	0	0	0	0	8	0
Pasture (%)	10	0	4	11	2	0
Other Lakes (%)	0	0	0	0	7	0
Houses in 1860 (No.)	0	0	0	4	1	0
Houses in 2007 (No.)	0	0	0	1	1	0

Plant and fell measurements complied from: Northern Ireland Forestry Service [a]; Sweeney (2007) [b]; Coillte Teoranta Ireland Forestry [c]. Other values estimated based on McElarney et al. (2010), aerial imagery (Environmental Protection Agency, 2012), historical mapping provided by the Ordnance Survey Ireland and from direct observation.

140

141   The coniferous forests of the study lakes were planted on upland areas of marginal

142   agricultural value, exhibiting predominantly peaty organic soils and heath moorland

143   vegetation (*Calluna, Erica, Molinia, Nardus spp*.). Previous land-use was constrained to low

144   stocks of mostly sheep (Renou & Farrell, 2005). Consequently, we expected the

145   disturbances associated with forest planting and felling to be distinct from those in local

146   lowland regions where eutrophication is more common (Reynolds & Petersen, 2000) due to

147   high levels of agriculture (Anderson, 1997). Specifically, planting of forests since the 1950s

148   on upland uncultivated soils such as infertile blanket peats required ploughing, planting and

149   application of fertilisers (Nieuwenhuis *et al.*, 2007). However the inability of organic soils to

150   adsorb phosphorus (P) meant fertilisation led to higher P losses into local catchment lakes in

151   upland lakes in NI when compared with Scottish lakes, particularly if catchments were

152   afforested (Foy & Bailey-Watts, 1998). Since the 1990s, harvesting of trees in Ireland has

153   increased exponentially (Department of Agriculture, 2014) with conifer harvesting followed

154   by exceptionally high concentrations of P, nitrogen (N) and (DOC) in drainage water,

155   probably reflecting the breakdown of brash which is left on site as a nutrient source for

156   replanting (Cummins & Farrell, 2003a, Cummins & Farrell, 2003b, Rodgers *et al.*, 2010,

157   Rodgers *et al.*, 2011). While in lowlands, agricultural applications of manure or nutrient

158   fertilisers (N, P) generally occur each year, upland Irish forestry tends to apply only P

159   fertilisers at the time of planting with the initial N requirements provided by mineralisation of

160   soil N stimulated by ploughing and precipitation inputs (Miller, 1981). In the studied lake

161   catchments, fertiliser N was not applied until after the forest canopy had closed, usually 12+

162   years after planting with the precise time interval being operationally determined and

163   influenced by the N content of the soil. Nitrogen was applied from the air typically as urea

164   pellets. Although the closed canopy and high biomass of trees exert a high demand for N,

165   direct contamination of surface waters within the forested area can occur (Gibson, 1976).

166   Catchment forestry records were compiled from archives at the Northern Ireland

167   Forest Service (Crockacleaven, Fadd), Coillte Teoranta Ireland Forestry (Anarry,

168   Carrownabanny, Afurnagh) and from a study by Sweeney (2007) (Lettercraffroe). Due to the

169   complex nature of forestry in these catchments, only the first year of tree plant and harvest

170   (felling) at each site could be reliably identified. Relative maximum (%) catchment land

171   cover as forest plantation (4-64%) and catchment to lake area ratios (3:1 to 15:1) were

172   estimated by tracing land-use using data from McElarney *et al.* (2010), aerial imagery

173   (Environmental Protection Agency, 2012), historical mapping to assess land cover in ~1880

174   prior to forestry activities and other land use (dating to the late 1800s) provided by the

175   Ordnance Survey Ireland. Additionally, where we had local first-hand knowledge of past

176   plantations that had not been accurately recorded in the archives (e.g. Fadd & Anarry), we

177   were able to make adjustments accordingly. Four catchments were planted in the 1960s

178   (Lettercraffroe, Crockacleaven, Anarry and Carrownabanny), and two catchments were

179   afforested in the 1990s (Afurnagh and Fadd). The Anarry and Crockacleaven catchments

180   were the first to be felled (in 1991), with later felling at Lettercraffroe (in 2002) and

181   Crockacleaven (in 2007). Post-1990 catchment plantations surrounding Afurnagh and Fadd

182   had not been felled prior to sediment coring. The catchment surrounding Fadd previously

183   had a small area of non-native forestry (included in the 6% afforested maximum land cover)

184   planted in the late 1970s but the young trees had been burnt prior to 1985 (field observation).

185   This small area was confirmed as previously being moorland using historical mapping dating

186   from the 1860s and some remnant isolated trees that survived the fire remain as evidence of

187   the past small plantation.

188   *Sediment coring*

189   HON-Kajak corers (Renberg, 1991) were used to obtain a continuous sediment

190   sequence (30-40 cm) from the deepest part of each lake during June to August 2007. All

191 cores had a visible and undisturbed water-sediment interface and were sectioned at 1-cm

192 intervals, except for Anarry sediments which were sectioned at 0.5-cm resolution.

193 Subsamples were stored either frozen at -20°C for fossil pigment analyses or refrigerated for

194 the remaining analyses.

Sediment chronology

196　　　Freeze-dried sediments from all cores were dated using ^{210}Pb, with additional samples

197 from Afurnagh analysed for ^{137}Cs. ^{210}Pb was measured by isotope-dilution alpha

198 spectrometry on an array of EG&G Nuclear Octête PCs, while ^{137}Cs was measured by

199 gamma spectrometry using EG&G germanium-crystal photon (well) detectors coupled to

200 digital gamma-ray spectrometers. Supported ^{210}Pb in each core was established from the

201 asymptote of total ^{210}Pb at depth (below the ^{210}Pb dating horizon) or by gamma assay of ^{214}Pb

202 in cores where supported values might be expected to vary owing to large changes in

203 sediment lithology (Loss on Ignition, LOI). Sediment chronologies were calculated using the

204 constant rate of supply (CRS) model with dating uncertainty estimated by first-order error

205 propagation (Binford, 1990, Appleby, 2001). The ^{210}Pb profile for Afurnagh was spliced

206 between two cores (collected in 2006 and 2007), as the original core did not quite reach the

207 ^{210}Pb dating horizon, and the dating model was fitted to the ^{137}Cs peaks for 1963 and 1986

208 (Chernobyl). For cores where samples extended beyond the ^{210}Pb dating horizon, dates were

209 extrapolated from the lowermost two intervals with measurable excess ^{210}Pb, which was more

210 appropriate than spline methods given the large changes in sediment accumulation found in

211 all cores. Dating results should therefore be considered only indicative prior to ~1820, with

212 results before this included to highlight pre-catchment disturbance. Dating results are

213 presented in McElarney *et al.* (2009), however since initial dating was published,

214 amendments to the Afurnagh model were made as additional samples for ^{137}Cs were analysed.

215 Dating was conducted at St. Croix Watershed Research Station, Minnesota.

216 *Pigment analysis*

217   Chlorophyll and carotenoid pigments were analysed using an Agilent 1200 series

218 HPLC with quaternary pump, autosampler, ODS Hypersil column (250 x 4.6 mm; 5µm

219 particle size), and photo-diode array detector as described in Leavitt and Hodgson (2001)

220 with the separation conditions as modified by Chen *et al.* (2001) and McGowan *et al.* (2012).

221 Pigments were calibrated using authentic standards (DHI, Denmark) and are expressed in

222 nmoles pigment g^{-1} organic matter, where the organic fraction was determined using weight-

223 loss-on-ignition (LOI) at 550ºC (Heiri *et al.*, 2001). Where present, the ultra-violet radiation-

224 (UVR-) absorbing pigment (scytonemin derivative) identified in Leavitt *et al.* (1997) was

225 divided by the sum of key carotenoids diatoxanthin, lutein-zeaxanthin and alloxanthin and

226 multiplied by 100 to derive a UVR index. Calibration in whole-lake experiments reveal that

227 this index increases as a linear function of depth of UVR penetration, such that higher values

228 indicate greater exposure to potentially-damaging UVR (Leavitt *et al.*, 1997).

229 *Stable isotope and elemental analysis*

230   Bulk non-acidified total carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes and

231 elemental % C and N measurements (for C/N ratios) were analysed using a ThermoQuest (F-

232 MAT) Delta^{PLUS}XL mass spectrometer coupled to a Carlo Erba elemental analyser and

233 following Savage *et al.* (2004). Isotopic ratios are expressed as per mille (‰) deviation from

234 atmospheric N$_2$ and organic V-PDB carbon standards, to a sample reproducibility of <0.3‰.

235 A correction was made for the Suess effect following Schelske and Hodell (1995) by

236 subtracting recorded δ^{13}C values of atmospheric CO$_2$ from the average pre-industrial value

237 (−6.49‰) for each sample based on its ^{210}Pb year according to the updated equation in

238 Verburg (2007).

239

Statistical analysis

241   Historical changes in gross algal community composition were estimated using

242 biomarker carotenoids including those from siliceous algae (diatoxanthin), cryptophytes

243 (alloxanthin), cyanobacteria (canthaxanthin) and all algae (β-carotene). Differences between

244 mean pigment concentrations in the pre- and post- planting periods were assessed using the

245 non-parametric Mann-Whitney U test in SPSS (v22), as pigment data did not conform to a

246 normal distribution. Timing of historical changes in potentially mixotrophic flagellates

247 (alloxanthin, cryptophytes), blooming-forming taxa (canthaxanthin, cyanobacteria), diatoms

248 (diatoxanthin), all algae (β-carotene), carbon and nitrogen stable isotopes (δ^{13}C & δ^{15}N),

249 carbon content (%C) and C/N ratios were determined for all sites with breakpoint analysis

250 using two segment piecewise linear regression (Toms & Lesperance, 2003) in the R package

251 'segmented' (Muggeo, 2008). The age of first tree planting was used to train the model and

252 included dates for Lettercraffroe (1960), Crockacleaven (1967), Anarry (1963),

253 Carrownabanny (1960), Afurnagh (1996) and Fadd lakes (1998). Ordinary least-squares

254 regression and two-segment piecewise linear regression (broken-stick model) was compared

255 using analysis of variance (ANOVA) to test if the breakpoint was significant. When

256 significant the breakpoint and its 95% upper and lower confidence intervals were plotted

257 against age. To explore how lake response varied with the extent of forestry, pigment ratios

258 of post-plant: pre-plant concentrations were estimated for both mean and maximum values

259 and were plotted against percentage catchment area planted with forests. To identify regional

260 temporal patterns, synchrony analysis (mean pairwise Pearson correlation coefficients (r)

261 from all possible core combinations, *S*) was performed on polynomial spline smoothed

262 nitrogen isotope (δ^{15}N) data interpolated at yearly intervals, for all lakes which were

263 individually Z-transformed and plotted against date (Patoine & Leavitt, 2006, Vogt *et al.*,

264 2011).

265 **Results**

266 *Pigments*

267   Concentrations of sedimentary alloxanthin (cryptophytes) and canthaxanthin

268 (cyanobacteria) increased significantly in the three lakes with the largest forest cover after

269 planting; Crockacleaven, Lettercraffroe and Anarry (Fig. 2, 3a-c).   There was a six-fold

270 increase in cryptophyte pigments (alloxanthin) (U=4, p<0.001) in Lettercraffroe, a four-fold

271 increase (U=38, p<0.001) in Crockacleaven, and a two-fold (U=33, P<0.001) increase at

272 Anarry following forest planting. Canthaxanthin concentrations also increased significantly

273 in these three lakes (U= range 0-83.5, p< 0.038-0.001), but their increases were quantitatively

274 less pronounced (39-116%) (Table 3). Ratios of maximum post-plant: pre-plant pigment

275 concentration were significantly correlated with the extent of catchment planting for both

276 alloxanthin (R^2-adj = 0.49, p<0.05) and canthaxanthin (R^2-adj = 0.62, p<0.05), although the

277 proportional increase was most evident at >50% of catchment planted (Fig. 2).
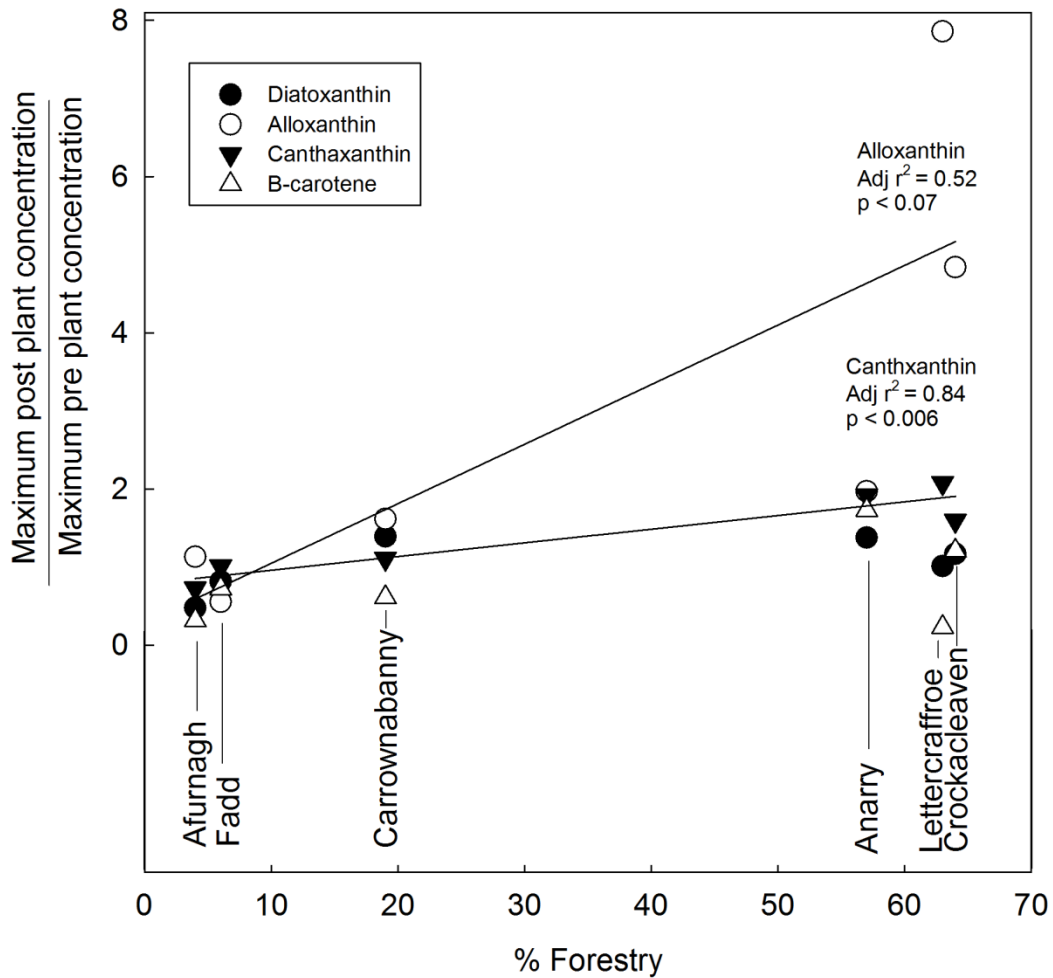
Figure 2: Ratio of maximum post-plant pigment concentration (since first plant) over maximum pre-plant (since 1900) pigment concentration against catchment percentage planted forestry. Linear regressions are presented for alloxanthin (cryptophytes) and canthaxanthin (cyanobacteria) pigments. A similar result was obtained when mean post-plant pigment concentration over mean pre-plant pigment concentrations were used (canthaxanthin adjusted $r^2 = 0.62$, p = 0.04; alloxanthin adjusted $r^2 = 0.49$, p = 0.07) (S. Figure 1).

a) Crockacleaven 64%

b) Lettercaffroe 63%

c) Anarry 57%

d) Carrownabanny 19%
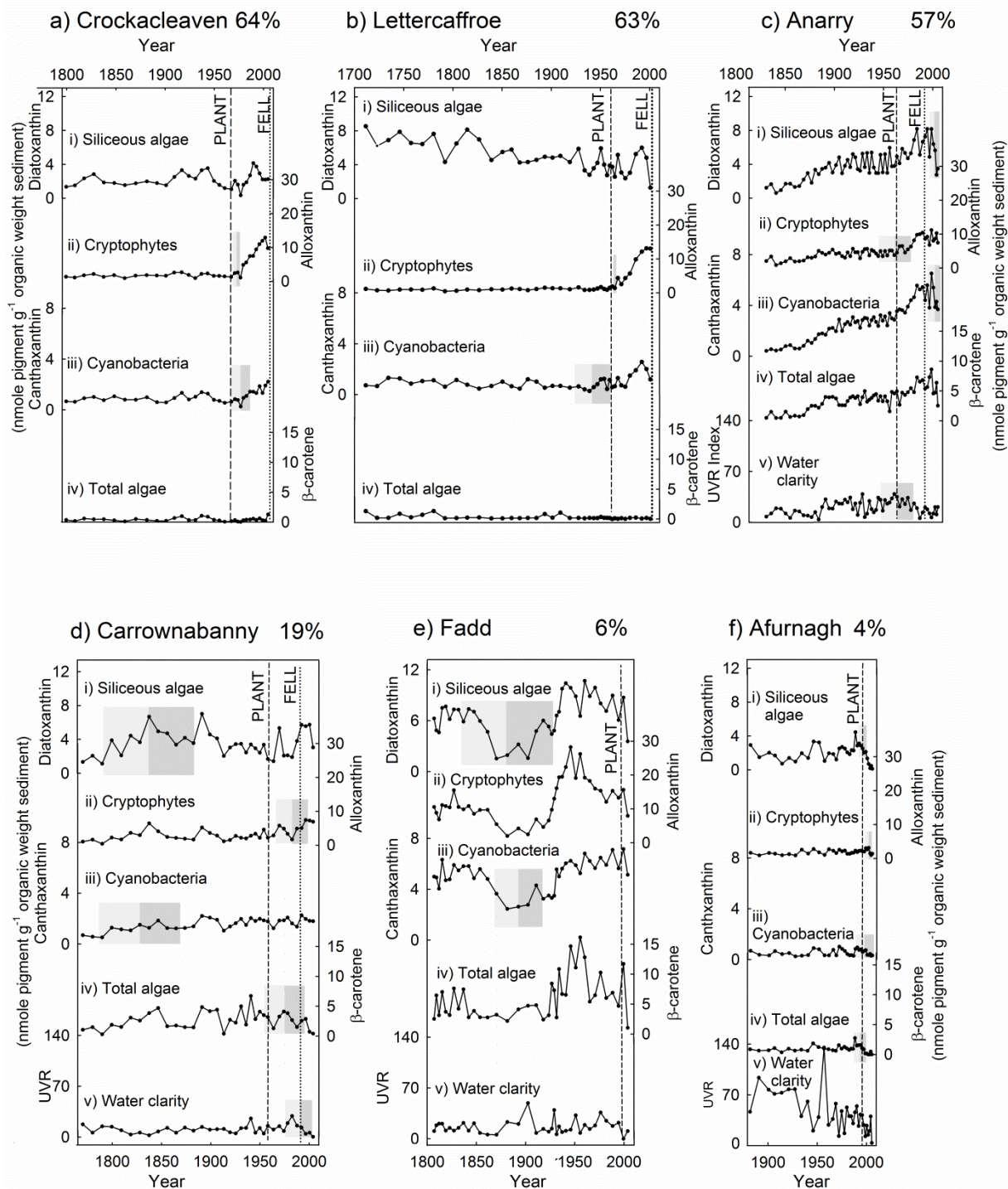
e) Fadd 6%

f) Afurnagh 4%

285

286

287

288 Figure 3: Changes in pigment concentrations for (a) Crockacleaven, (b) Lettercraffroe, (c)

289 Anarry, (d) Carrownabanny, (e) Fadd and (f) Afurnagh. Variables include: (i) siliceous algae

290 (diatoxanthin), (ii) cryptophytes (alloxanthin), (iii) cyanobacteria (canthaxanthin), (iv) total

291 algae (β-carotene) and (v) water clarity inferred from the (UVR) index. Date of first planting

292 (indicated by PLANT), and date of first felling (indicated by FELL). 95% confidence interval

293 breakpoints highlighted (light shading = below breakpoint; dark shading = above breakpoint).

294 Breakpoints presented where ANOVA analysis indicated the broken stick model was more

295 appropriate than the linear model ($p<0.05$) (S. Table 1 & 2). Maximum percentage forestry is

296 indicated at the top right hand of each sub-plot.

Table 3: Mean concentration (±SD) and non-parametric Mann–Whitney U test values before and after afforestation for selected key pigment variables (diatoxanthin, alloxanthin, canthaxanthin and β-carotene).

			Crockacleaven	Lettercraffroe	Anarry	Carrownabanny	Fadd	Afurnagh
First planting			1967	1960	1963	1960	1996	1998
Diatoms (diatoxanthin)	Mean concentration (±SD)	before	2.1±0.69	5.4±1.6	3.3±1.35	3.5±1.43	6.5±2.36	2.2±0.85
		after	2.2±1.0	3.7±1.5	5.8±1.58	3.7±1.8	6.1±3.7	1±0.84
	U		117	73	99	121.5	32	31
	P		0.65	0.015*	<0.001**	0.768	0.822	0.005*
Cryptophytes (alloxanthin)	Mean concentration (±SD)	before	1.7±0.48	1.0±0.29	3.8±1.25	2.6±1.35	12.5±6.25	1.8±0.57
		after	6.8±4.1	6.8±4.7	7.9±2.1	5.0±1.9	11.8±5.4	2.1±0.9
	U		38	4	33	41	34	75
	P		<0.001**	<0.001**	<0.001**	0.001*	0.922	0.427
Filamentous cyanobacteria (canthaxanthin)	Mean concentration (±SD)	before	0.89±0.25	0.80±0.30	2.08±0.93	1.47±0.47	5.02±1.23	0.56±0.24
		after	1.24±0.55	1.3±0.69	4.50±0.91	1.78±0.31	6.14±1.43	0.45±0.18
	U		72	83.5	0	81.5	19	73.5
	P		0.033*	0.038*	<0.001**	0.087	0.266	0.379
All algae (β-carotene)	Mean concentration (±SD)	before	0.4±0.28	0.4±0.36	2.9±1.33	2.8±1.57	6.1±3.56	1.1±0.49
		after	0.4±0.32	0.1±0.08	5.4±1.56	2.3±1.28	6.4±7.57	0.2±0.32
	U		113	52	69	108	33	11
	P		0.548	0.001*	<0.001**	0.454	0.871	<0.001**
	No. samples	before	20	30	18	10	36	7
		after	13	10	42	26	2	27

*, p < 0.05; **, p < 0.001   All concentrations in nmol pigment g^{-1} organic weight sediment.

297   Breakpoint analysis confirmed that fossil alloxanthin concentrations changed in the

298   three lakes with the most intense forestry close to the timing of forest planting: Lettercraffroe

299   in 1964 (95% confidence interval (CI), 1962-1966), immediately after the 1960 planting (R^2-

300   adj = 0.97; F = 447.92; p<0.001), Crockacleaven in 1973 (95% CI 1969-1976) after 1967

301   planting (R^2-adj = 0.93; F = 133.14; p<0.001), and Anarry in 1961 (95% CI 1945-1977)

302   which was close to 1963 planting (R^2-adj = 0.76, F = 14.5, p<0.001) (Fig. 3, S. Table 1). In

303   contrast, the breakpoints for canthaxanthin increases were less clear cut with wide confidence

304   limits and therefore not so closely aligned to the commencement of afforestation. The

305   breakpoint occurred at 1942 in Lettercraffroe (95% CI 1924-1960) compared to tree planting

306   starting in 1960 although the 95% CI of 1924-1960 just encompasses the start of planting

307   (R^2-adj = 0.43; F = 14.86, p<0.001). In Crockacleaven the canthaxanthin breakpoint in 1977

308   was after the 1967 planting date although again the 95% CI of the breakpoint 1967-1987 just

309   overlaps with the planting year after 1967 planting R^2-adj = 0.63; F=20.13; p<0.001. In

310   Anarry there was initially no agreement with planting as the breakpoint for canthaxanthin

311   was not until 2001 (95% CI 1994-2007), which was coincident with felling and well after the

312   first planting of 1963 (R^2-adj = 0.87, F = 4.4, p<0.05) (Fig. 3, S. Table 1). However, there

313   was agreement when recent post-fell samples were removed from the model resulting in a

314   breakpoint of 1962 (95% CI 1947-1977) close to 1963 planting (R^2-adj = 0.90; F = 11.33).

315   Interestingly, total algal abundance as β-carotene exhibited no clear relationship with forest

316   planting in these three heavily impacted catchments (Fig. 3a-c), while UVR pigments were

317   absent from Crockacleaven or Lettercraffroe (Fig. 2a,b), but increased in Anarry sediments

318   after ~1800 until the initial forestry planting (Fig. 3c).

319   Algal communities were less significantly affected by catchment afforestation in the

320   three remaining lakes where forest plantations accounted for <20% of catchment area (Fig.

321   3d-f). Carrownabanny, Fadd and Afurnagh all featured variable pigment profiles and UVR
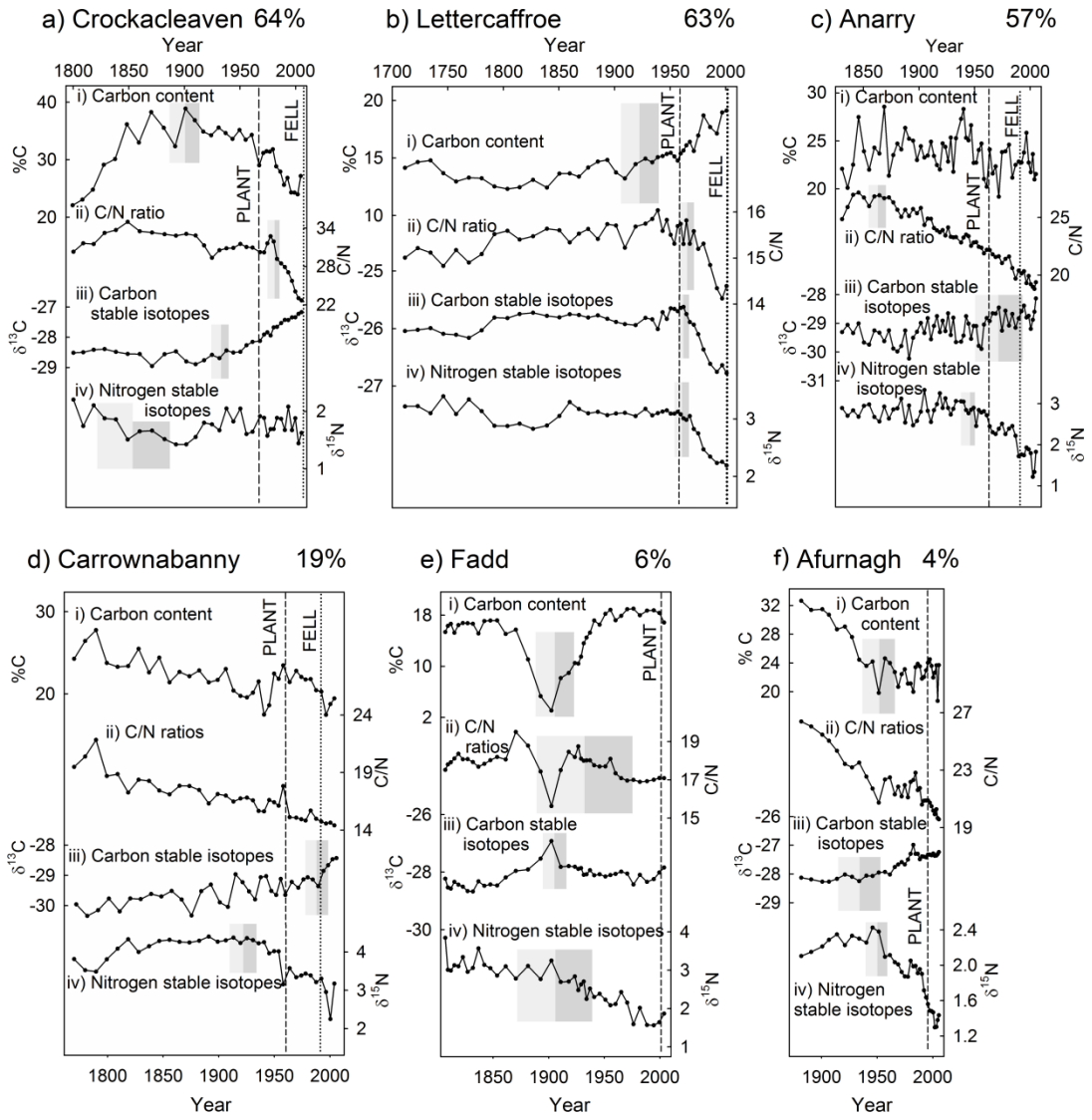
322   indices both before and after forest planting (Fig 3d-f). Unlike the more heavily managed

323   catchments, fossil alloxanthin or canthaxanthin content exhibited little directional change in

324   Carrownabanny and planting was too recent in control sites Fadd and Afurnagh to test for the

325   effect of planting. In general, breakpoints for alloxanthin occurred slightly after the onset of

326   forest planting in Carrownabanny and Afurnagh, but in Fadd the breakpoint was not

327   significant (Fig. 3d-f, S. Table 2). Although there was a breakpoint relationship between

328   diatoxanthin (diatoms), canthaxanthin (cryptophytes) and β-carotene (total algae) and plant

329   date in Afurnagh, the concentrations were highly variable before planting, suggesting that

330   changes of similar magnitude to forestry had precedent in the past (Fig. 3f, S. Table 2).

331   Fossil pigment concentrations varied considerably through time in most lakes prior to

332   forest planting within the 20th century (Fig. 3). For example, in Lettercraffroe, there was a

333   gradual decline in diatoxanthin (diatoms) from ~1700 to ~2000, with pulses of β-carotene

334   (total algae) throughout the 1700s and ~1900 (Fig 3b). In contrast, Crockacleaven exhibited

335   contemporaneous peaks of diatoxanthin (mainly diatoms) and β-carotene between ~1900 and

336   ~1950 (Fig. 3a), whereas Anarry featured a gradual increase in all pigments from the start of

337   the record prior to 1963 planting (Fig. 3c). Fossil pigments in Carrownabanny and Afurnagh

338   fluctuated considerably throughout their records (Fig. 3d,e) with marked declines in Fadd

339   between ~1860 and ~1910 followed by an increase in alloxanthin pigment peaking around

340   ~1940 (Fig. 3f).

341   *Geochemistry*

342   Geochemical and isotopic proxies suggest that afforestation resulted in changes in the

343   character and provenance of sedimentary carbon in lakes with greatest forest cover (Fig. 4).

344   For example, sedimentary C/N ratios declined following initial tree planting in lakes

345   with >50% of catchment forest cover (Fig. 4a-c), while trends were less marked in Fadd (4e)

346   (6% afforestation) and declined before planting in Anarry (57% afforestation) and Afurnagh

347   (4% afforestation) (Fig. 4c, f). In contrast, $\delta^{13}C$ values increased in all lakes after plantations

348   were established, except intensively forested Lettercraffroe where sedimentary carbon isotope

349   ratios were sharply depleted after planting (Fig. 4b). At Lettercraffroe breakpoints for $\delta^{13}C$

350   ratios (1962, 95% CI 1957-1967), $\delta^{15}N$ (1961, 95% CI 1954-1967) and C/N ratios (1965, CI

351   1958-1971) were all clearly coincident with tree planting (all $p<0.001$) (Fig. 4b, S. Table 1).

352   However, in Crockacleaven no breakpoints were perfectly coincident with planting; rather the

353   breakpoint for C/N was slightly after planting (1980, 95% CI 1974-1985), while in Anarry

354   only the breakpoint for $\delta^{13}C$ was coincident with forestry (1972, 95% CI 1950-1993) (Fig.

355   4a,c; S. Table 2). When plotted together (Fig. 5), lake zones defined by C/N ratios and $\delta^{13}C$

356   values revealed that afforestation typically produced changes characteristic of increased algal

357   production in dilute lakes (lower C/N, enriched $\delta^{13}C$), with the exception of Lettercraffroe

358   (lower C/N but depleted $\delta^{13}C$ (Fig. 4b)) and Fadd for which there were no separation of pre

359   and post planting samples.

a) Crockacleaven 64%

b) Lettercaffroe 63%

c) Anarry 57%

d) Carrownabanny 19%

e) Fadd 6%

f) Afurnagh 4%

24

362   Figure 4: Changes in bulk and isotopic measures for (a) Crockacleaven, (b) Lettercraffroe, (c)

363   Anarry, (d) Carrownabanny, (e) Fadd and (f) Afurnagh. Variables include: (i) carbon content

364   determined by elemental analysis on bulk carbon (%C), (ii) C/N ratio, (iii) δ^{13}C, and (iv) δ^{15}N.

365   Date of first planting (indicated by PLANT), and date of first felling (indicated by FELL). 95%

366   confidence interval breakpoints highlighted (light shading = below breakpoint; dark shading

367   = above breakpoint). Breakpoints presented where ANOVA analysis indicated the broken

368   stick model was more appropriate than the linear model ($p < 0.05$) (S. Table 1 & 2).

369
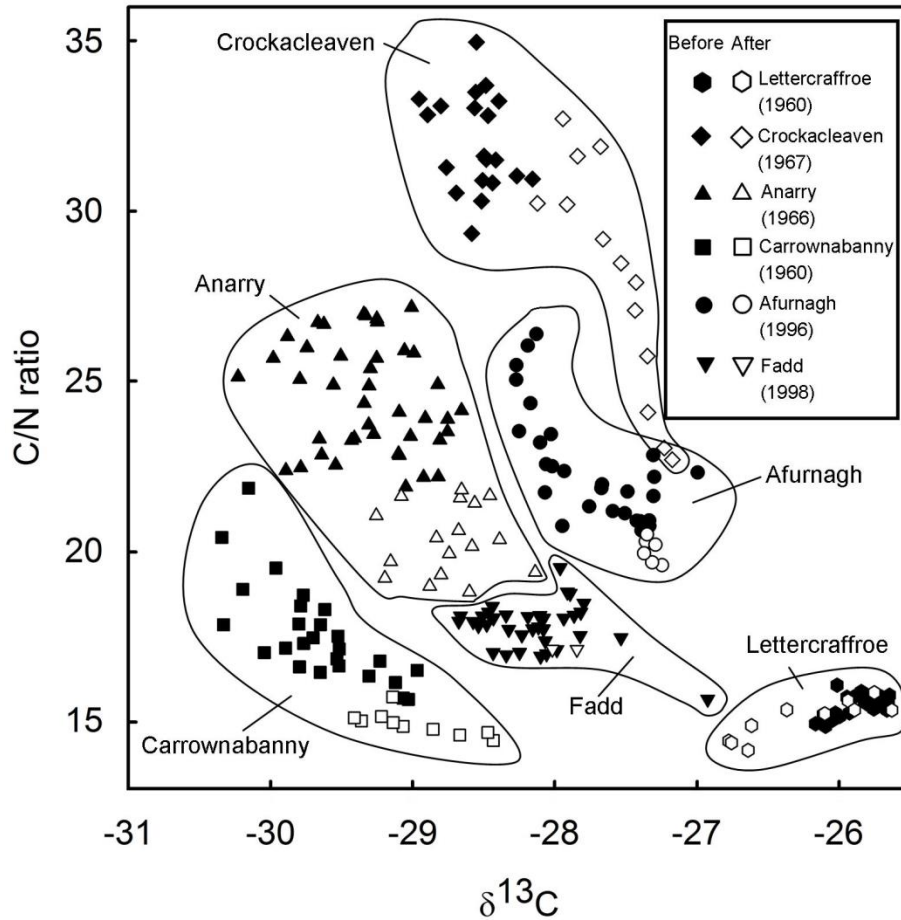
Figure 5: Plot of C/N ratio against $\delta^{13}C$ (corrected for the Suess effect) for samples from Lettercraffroe (hexagon), Crockacleaven (diamond), Anarry (upwards triangle), Carrownabanny (square), Afurnagh (circle), and Fadd (downwards triangle). Filled symbols denote sample prior to afforestation, open symbols denote after afforestation. Zones occupied by each lake are encircled to aid interpretation and brackets denote the first plant year.

375   Overall, nitrogen isotope values declined during the 20th century, with relatively high

376   rates of depletion being recorded in many sites after ca. 1950 (Fig. 4 & 6). In the case of

377   Lettercraffroe, Anarry, and Carrownabanny, δ^{15}N declined during forest planting; however,

378   while Crockacleaven and Fadd exhibited few pronounced changes, declines at Afurnagh

379   clearly preceded forest planting. The declines in δ^{15}N were found to be highly synchronous

380   in Afurnagh, Lettercraffroe, Carrownabanny, Anarry and Fadd (S =0.94, p<0.001), and to a

381   lesser extent when Crockacleaven was included in the model (S=0.58, p <0.001) (Fig. 6).

382   When ratios of mean and maximum post-plant: pre-plant δ^{15}N were plotted against

383   percentage forestry, a clear trend was established between higher planted forestry and δ^{15}N

384   (maximum R^2-adj = 0.64, p <0.03) (S. Fig. 2).
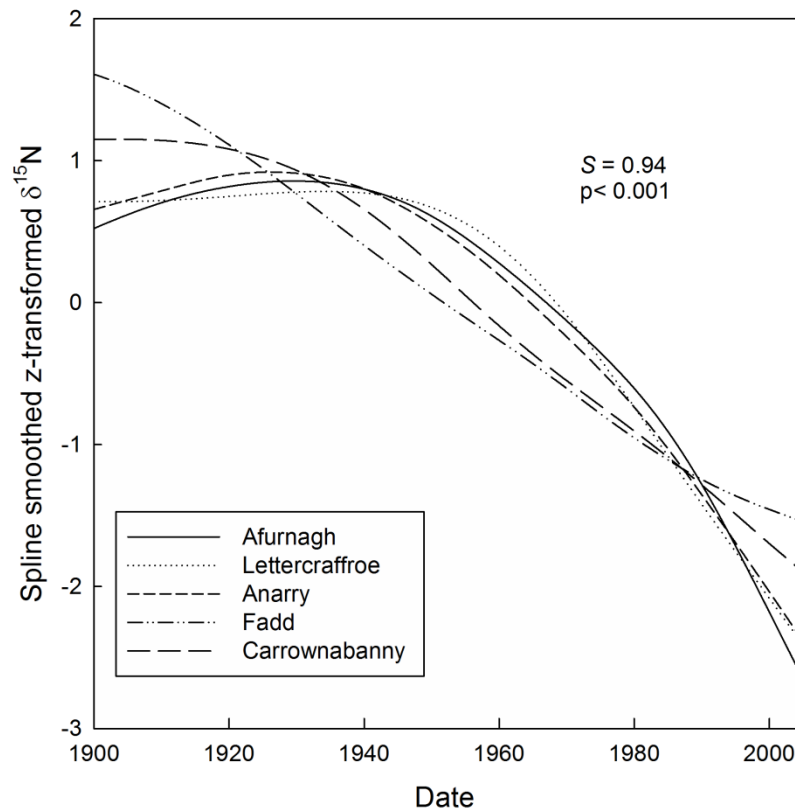
Figure 6: Synchrony analysis of polynomial spline smoothed nitrogen isotope ($\delta^{15}N$) data interpolated at yearly intervals and Z-transformed against date for Afurnagh, Lettercraffroe, Anarry, Fadd and Carrownabanny, with significance established using 999 Monte Carlo randomizations. When Crockacleaven was included in the model the results indicated lower, but still significant synchrony ($S = 0.58$, $p < 0.001$).

391   Geochemical and isotopic parameters also exhibited high temporal variability prior to

392 forest planting. For example, in Anarry, carbon content varied between ~29% and 20%

393 throughout the record, whereas analysis of sediments from Carrownabanny and Afurnagh

394 recorded a decline in C content prior to the planting of the forests (Fig. 4c,d,f). Similarly,

395 C/N ratios declined and $\delta^{13}C$ values increased in Anarry, Carrownabanny and Afurnagh well

396 before planting (Fig. 4c,d,f). Across Carrownabanny, Fadd and Afurnagh, no breakpoints

397 were coincident with planting and only the change in $\delta^{13}C$ in Carrownabanny was coincident

398 with felling (1998, 95% CI 1978-1998) (Fig. 4d-f; S. Table 2). In Fadd, a sharp decline in

399 carbon content, C/N ratios and an increase in $\delta^{13}C$ values occurred ~1890, followed by a

400 return to previous levels by ~1940 (Fig. 4e). Similarly, temporal variation in $\delta^{13}C$ and $\delta^{15}N$

401 values was generally lower in the 19th century than during the 20th century.

Discussion

In lakes where forestry exceeded 50% of the catchment land cover, the timing of algal community change is consistent with the hypothesis that forest plantations had a significant impact on algal abundance and gross community composition. In particular, cryptophytes (as alloxanthin) and to a lesser extent colonial cyanobacteria (as canthaxanthin) increased as a function of the percentage of afforestation in the lake catchment (Figure 2). In contrast, we found little evidence of forestry impacts in lakes with lower forest cover (<20%), although all sites exhibited substantial and individualistic variability in pigment and isotopic records prior to initiation of conifer plantations. Together, these findings suggest that water quality in upland lakes can be threatened by catchment forestry if planting represents more than half of the catchment area.

Limnological consequences of intensive conifer plantations

The significant increases in concentrations of fossil canthaxanthin and alloxanthin after tree planting in Crockacleaven, Lettercraffroe and, to a lesser extent, Anarry catchments suggest that forest planting was a major factor regulating growth of cryptophytes and cyanobacteria in these lakes (Fig. 3). Consistent with this interpretation, C/N ratios declined in these lakes immediately after forest planting indicating that more of the sedimentary carbon was derived from algal sources (Meyers & Teranes, 2001), while in most cases $\delta^{13}C$ values increased <1‰ from depleted values between −28 and −30‰. In most lakes with enrichment, this meant $\delta^{13}C$ isotopes moved to values characteristic of algal respired CO_2 (ca. −27‰) (Meyers & Teranes, 2001). However, in Lettercraffroe there was a decline in $\delta^{13}C$ after planting as previous values were higher, indicating a switch in algal source (Figure 5).

Management of afforested catchments may favour enhanced algal abundance through runoff of fertilisers. Commercial forestry in ROI and NI has often fertilised soils at rates of

426   50-90 kg P/ha (Dickson & Savill, 1974) which exceed the P-binding capacity of such iron-

427   and aluminium-poor soils (Maguire *et al.*, 2001). Disproportionate increases in cyanobacteria

428   following elevated nutrient influx have been recorded in many regions of the northern

429   hemisphere (Taranu *et al.* 2015), and reflect multiple concomitant fertilisation mechanisms

430   such as deposition of atmospheric nutrients (Holtgrieve *et al.*, 2011), agriculture (Battarbee *et*

431   *al.*, 2005, Bunting *et al.*, 2007, Moorhouse *et al.*, 2014), and urbanisation (Leavitt *et al.*, 2006,

432   McGowan, 2016). Although total algal biomass usually increases with eutrophication,

433   increases in phytoplankton production associated with fertilisation may out-compete benthic

434   algae, and compress the photic zone in the water column, leading to changes in overall algal

435   habitat and community composition (McGowan *et al.*, 2005). Although speculative, we infer

436   that such shifts may underlie the observation that sharp increases in cryptophytes and

437   cyanobacterial abundance after forest planting was not marked by a concomitant increase in

438   total algal deposition (as β-carotene).

439   　　　Forestry planting and felling may have also favoured development of mixotrophic

440   populations by increasing influx of terrestrial organic matter to upland lakes through several

441   mechanisms (Jansson *et al.*, 2000, Jansson *et al.*, 2001). In general, forestry planting and

442   felling may increase the export of dissolved organic matter (DOM) and dissolved organic

443   carbon (DOC) to lakes and streams (Carignan *et al.*, 2000, O'Driscoll *et al.*, 2006, Schelker *et*

444   *al.*, 2012). First this increased influx of DOM might directly fertilise potentially mixotrophic

445   algae such as cryptophytes and cyanobacteria (Jones, 2000, Burkholder *et al.*, 2008). Second,

446   elevated DOM and particular organic matter (POM) influx can stimulate primary production

447   indirectly by providing a substrate for heterotrophic bacteria (Tranvik, 1990) which can either

448   be ingested by phagotrophic heterotrophs (Isaksson *et al.*, 1999, Jones, 2000) or which may

449   provide dissolved nutrients to autotrophs after consumption by herbivores (Sanders *et al.*,

450   1990). Third, increased DOM influx could reduce light penetration and favour highly motile

31

451   and predominantly planktonic (cryptophytes) or buoyant (colonial cyanobacteria) taxa which

452   can better exploit shallow photic zones (Ojala *et al.*, 1996, Staehr *et al.*, 2010), compared

453   with dinoflagellates and chrysophytes. Consistent with this last mechanism, we note that

454   fossil diatom assemblages switch from predominantly benthic to more planktonic forms in

455   Crockacleaven and Lettercraffroe following plantation development (McElarney *et al.*, 2009).

456   While it is possible that precipitation-derived increases in DOC runoff may also occur in

457   these lakes (Monteith *et al.*, 2007), the asynchronous timing of cryptophyte expansion argues

458   against a coherent regional driver of algal community change.

459   *Other controls of algal abundance*

460   Upland lakes of the north west of Ireland exhibited substantial variation in algal

461   abundance independent of the effects of catchment afforestation, likely reflecting the

462   combined effects of regional and local factors. Among regional stressors, the island of

463   Ireland may have been impacted by recent atmospheric warming since c. 1986 (Anderson *et*

464   *al.*, 2012) and changes in hydrology associated with the NAO (George *et al.*, 2004, Adrian *et*

465   *al.*, 2006), altered influx of nitrogen due to deposition of atmospheric Nr (Holtgrieve *et al.*,

466   2011), elevated influx of terrestrial DOM (Monteith *et al.*, 2007), or acidic precipitation and

467   recovery (Battarbee *et al.*, 1990, Jones *et al.*, 1993, Flower *et al.*, 1994). In addition, peat

468   extraction for fuel has been practised regionally since prehistoric times, but peaked during the

469   19th century population expansion, and again in the 1940s with the introduction of

470   mechanized peat harvest (Renou & Farrell, 2005). While these factors did not obscure the

471   effects of afforestation in catchments with >50% of land cover conversion to forests (Fig. 3a-

472   c), such processes may have had a mediating effect on less forestry-affected sites, as well as

473   all basins prior to, and during the advent of forest plantations.

474   All lakes exhibited evidence of local land-use disturbance prior to planting of forests,

475   but such events were particularly pronounced in lakes with lower cover of coniferous trees.

476   For example, C/N ratios slowly declined in Anarry, Carrownabanny and Afurnagh suggesting

477   increased algal contributions before planting, while there were multiple fluctuations in all

478   proxies in Afurnagh and Fadd. These changes likely reflect the combined impacts of upland

479   grazing and peat cutting, rather than lowland agricultural and urbanisation factors, as these

480   upland catchments were of rough pasture and moorland unsuitable for agriculture prior to

481   afforestation (Renou & Farrell, 2005). Extensive upland grazing by sheep is known to have

482   contributed to the decline of *Calluna* on the heath moorland of Ireland, elevated local soil

483   erosion (Stevenson & Thompson, 1993), and contributed to increased sediment yields

484   despite low sheep stocking densities (Evans, 1997). Similarly, peat cutting directly

485   destabilises catchments, increasing sediment and nutrient runoff (Renou-Wilson & Farrell,

486   2007) and provides an additional mechanism to account for the perturbations across multiple

487   proxies and sites before planting (Carrownabanny, Afurnagh and Fadd). Notable is the

488   increase in alloxanthin pigment in Fadd prior to forestry (peaking in the 1940s), a pattern

489   which may record increased inputs of terrestrial organic matter and, consequently,

490   mixotrophy (Fig. 3e). Additionally, catchment to lake area ratios (Table 2) which are slightly

491   larger in the lakes with lower percentage afforestation (Carrownabanny, Afurnagh, Fadd)

492   may increase the potential in these lakes for non-forestry catchment disturbance events,

493   which are usually highly localised, to be recorded.

494   Although acidification has been observed previously in Irish upland lakes (Flower *et*

495   *al.*, 1994), we did not find consistent sedimentary evidence of the effects of regional acid

496   deposition: algal pigment changes were either clearly concomitant to forestry, or did not

497   exhibit a common pattern among lakes during the interval when acidification would be

498   expected to be evident in the mid-19th century (as early as the 1860s) (Flower *et al.*, 1994,

33

499   Aherne & Curtis, 2003, O'Dwyer & Taylor, 2010). Although, Crockacleaven and

500   Lettercraffroe (pH 6.3) (Table 1) presently have a lower pH than other sites, and exhibit some

501   evidence from fossil diatoms of recovery from acidification (N.J. Anderson, unpublished

502   data), these chemical conditions are unlikely to be sufficiently acidified to affect gross algal

503   community composition.

504   Declines in δ^{15}N in five of the six lakes were highly synchronous ($S = 0.94$, p<0.001)

505   which point to broad regional drivers of change (Fig. 6). Declines were also moderately

506   synchronous ($S = 0.58$, $p < 0.001$) if all six lakes were considered. The intensity of the North

507   Atlantic Oscillation (George $et\ al.$, 2004) and the north-south movements of the Gulf Stream

508   (Taylor, 1996) have been linked to coherent regional forcings of algae in the UK Lake

509   District (McGowan $et\ al.$, 2012, Moorhouse $et\ al.$, 2014) and nitrate deposition in Ireland

510   (Jennings & Allott, 2006, Anderson $et\ al.$, 2012). Since the breakpoint in δ^{15}N decline is only

511   coincident with planting in one lake (Lettercraffroe) we do not interpret the broad pattern of

512   δ^{15}N depletion to be driven by catchment land use. Instead, this highly synchronous decline

513   in δ^{15}N may be related to atmospheric deposition of Nr (Holtgrieve $et\ al.$, 2011) and-or

514   DOM-N influx associated with post-1970 changes in rainfall patterns and DOM runoff.

515   Increased export of DOC from upland catchments in the Northern Hemisphere (Freeman et

516   $al.$, 2001) have been associated with declines in atmospheric deposition of anthropogenic

517   sulphur and climate mediated sea salt deposition (Monteith $et\ al.$, 2007). Additionally, a

518   notable increase in DOC has been recorded in Northern Ireland upland softwater lakes

519   (McElarney $et\ al.$, 2010) so both the direct deposition of Nr and elevated DOM runoff could

520   alter N isotope ratios. In general, these effects should be most pronounced in systems with

521   intrinsically low N content (Holtgrieve $et\ al.$, 2011), or those receiving particularly high

522   influx of Nr (Galloway $et\ al.$, 2008). Regardless of the precise pathway of N influx,

523   synchronous declines in $\delta^{15}N$ during the 20th century are mostly consistent with regional

524   mechanisms (Hu *et al.*, 2014) rather than upland forest planting and felling activities.

525   *Recommendations for forestry management*

526   Our study provides clear evidence that forestry planting in upland catchments leads to

527   a major reorganization of algal communities (cryptophytes, cyanobacteria) in lakes with >50%

528   catchment afforestation. These findings suggest that forestry managers can identify lakes

529   likely to be impacted by plantation through a simple estimate of proportional land use. At

530   sites where catchments are 50% planted or more, it is especially important that strategies are

531   enacted to reduce potential damage to aquatic ecosystems, including application of

532   discontinuous forestry, harvesting only on dry soils, maintenance of marginal buffer strips

533   and brash-mats. Elsewhere, these procedures have been shown to most effectively reduce

534   nutrient, soil and suspended solid loss (Giller & O'Halloran, 2004, Rodgers *et al.*, 2011, Xiao

535   *et al.*, 2012). In Ireland upland catchment buffer strips have been confirmed to help reduce

536   the impact on aquatic ecology (Ryder *et al.*, 2011), with a recommendation for a more

537   targeted, species-specific fertilisation to be applied gradually near tree roots, rather than

538   spread openly on bare soil to minimise wastage and subsequent leaching (Renou-Wilson &

539   Farrell, 2007). The Irish Forest Service now aim to reduce fertilisation at planting to 42 kg

540   P/ha (Cummins & Farrell, 2003b). Such activities will likely help reduce cyanobacteria

541   blooms and toxicity in catchment lakes, helping to maintain water quality both for aquatic

542   communities and downstream water management.

543   Detailed phytoplankton experimentation studies on impacted lakes may also help

544   elucidate the role of potential cryptophyte mixotrophy in these dystrophic, anthropogenically

545   disturbed humic forest lakes. Future research needs to better understand the mechanisms that

546   promote mixotrophy and help guide our understanding of carbon and nutrient dynamics in

547   impacted lakes (Jansson, 1998, Jansson *et al.*, 2000, Jones, 2000). Efforts to increase forest

548   cover in the ROI to 17% by 2030 (Renou & Farrell, 2005) are a response to the growing

549   need for timber and the effectiveness of afforestation to sequester carbon and meet emission

550   reduction targets (Fuchs *et al.*, 2013, Bárcena *et al.*, 2014). However our study demonstrates

551   for the first time for both cryptophyte and cyanobacterial algal communities together that

552   forestry planting is capable of altering lake ecosystem structure and function. Such

553   continuous pressure for forest management is unlikely to abate, making it increasingly

554   important to understand how intensive management practices like upland forestry can, if

555   improperly managed interact with regional stressors to change and modify upland aquatic

556   ecosystems.

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Supporting information

833   **Supporting information**

834   1. Supporting information pack containing additional summary diagram figures (S. Fig 1 & 2)

835   and breakpoint summary tables (S. Table 1 & 2).