

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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27 disturbance, land-use change.

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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). <sup>210</sup>Pb dated sediment cores were analysed for carotenoid pigments from  
35 algae, stable isotopes of bulk carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ), 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 ( $\beta$ -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.

## 48 **Introduction**

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

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

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 brush, 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

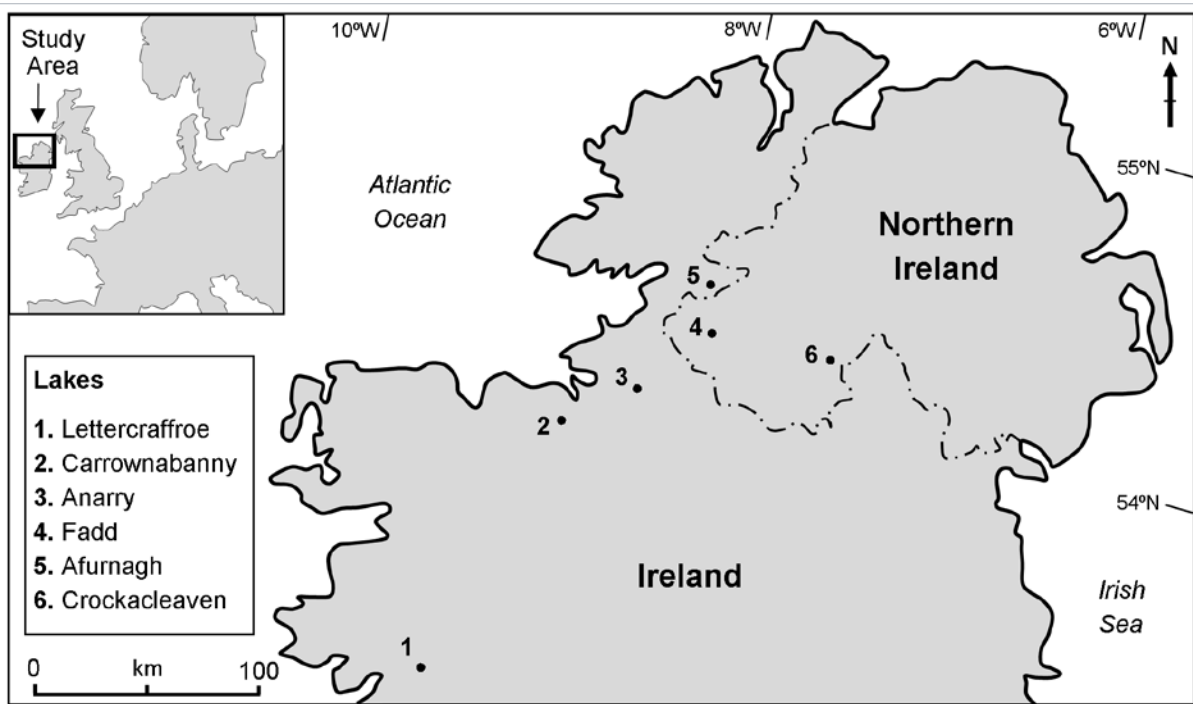
97 altered in upland lakes. Such effects in landscapes where lakes are abundant, as in Ireland,  
98 have the potential to influence regional carbon fluxes (Cole *et al.*, 2007).

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 (chlorophyll, carotenoids) from algae and cyanobacteria, as well as  
102 geochemical proxies of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) cycling over the past ~150 years in  
103 dated 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.



121

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  $\mu\text{g L}^{-1}$  and total oxidised nitrogen, TON 0.1-1.1  $\text{mgL}^{-1}$ ), but all had relatively low  
137 phytoplankton biomass (chlorophyll *a* 2.7-9.1  $\mu\text{g L}^{-1}$ ), high dissolved organic carbon (DOC)  
138 concentrations 8-16.1  $\text{mg C L}^{-1}$  and circumneutral pH from 6.3-7.9 (Table 1).



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

	<b>Crockacleaven</b>	<b>Lettercraffroe</b>	<b>Anarry</b>	<b>Carrownabanny</b>	<b>Fadd</b>	<b>Afurnagh</b>
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 <sup>(a)</sup>	83	102	138	123
Lake area (ha)	4	78	12	7.2	6	7
Max depth (m)	5.5	17.9 <sup>(a)</sup>	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-Cambrian Quartzite, Gneisses and Schist	Pre-Cambrian Quartzite, Gneisses and Schist. Lake on sandstone.	Sandstone, shales	Pre-Cambrian Quartzite, Gneisses and Schist
Conductivity @20°C ( $\mu\text{Scm}^{-1}$ )	53.9	82.5	85.0	120.3	82.6	66.6
Alkalinity (mequiv $\text{l}^{-1}$ )	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 <sub>2</sub> (mg $\text{l}^{-1}$ )	1.6	0.6	1.4	0.3	0.4	1.7
TP ( $\mu\text{g l}^{-1}$ )	65.5	10.8	37.3	56	11	22.5
TON (mg $\text{l}^{-1}$ )	1.1	0.2	0.1	0.3	0.5	0.0
Chlorophyll <i>a</i> ( $\mu\text{g l}^{-1}$ )	6.0	9.1	5.0	3.1	3.4	1.4
DOC (mg $\text{l}^{-1}$ )	14	-	-	16.1	8	11.4

Water chemistry measurements compiled from: McElarney *et al.* (2009) and McElarney *et al.* (2010), AFBI sampling and EPA (Ireland) sampling for Water Framework Directive compliance. <sup>(a)</sup> Denotes lake variables compiled from De Eyto *et al.* (2002). Abbreviations: silica (SiO<sub>2</sub>), 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.

<b>Lake</b>	<b>Crockacleaven</b>	<b>Lettercraffroe</b>	<b>Anarry</b>	<b>Carrownabanny</b>	<b>Fadd</b>	<b>Afurnagh</b>
First plant (year)	1967 <sup>(a)</sup>	1960 <sup>(b)</sup>	1963 <sup>(c)</sup>	1960 <sup>(c)</sup>	1996 <sup>(c)</sup>	1998 <sup>(a)</sup>
First fell (year)	2000 <sup>(a)</sup>	2002 <sup>(b)</sup>	1991 <sup>(c)</sup>	1991 <sup>(c)</sup>	-	-
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 compiled from: Northern Ireland Forestry Service <sup>(a)</sup>; Sweeney (2007) <sup>(b)</sup>; Coillte Teoranta Ireland Forestry <sup>(c)</sup>. 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.

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.

#### 195 *Sediment chronology*

196 Freeze-dried sediments from all cores were dated using  $^{210}\text{Pb}$ , with additional samples  
197 from Afurnagh analysed for  $^{137}\text{Cs}$ .  $^{210}\text{Pb}$  was measured by isotope-dilution alpha  
198 spectrometry on an array of EG&G Nuclear Octète PCs, while  $^{137}\text{Cs}$  was measured by  
199 gamma spectrometry using EG&G germanium-crystal photon (well) detectors coupled to  
200 digital gamma-ray spectrometers. Supported  $^{210}\text{Pb}$  in each core was established from the  
201 asymptote of total  $^{210}\text{Pb}$  at depth (below the  $^{210}\text{Pb}$  dating horizon) or by gamma assay of  $^{214}\text{Pb}$   
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  $^{210}\text{Pb}$  profile for Afurnagh was spliced  
206 between two cores (collected in 2006 and 2007), as the original core did not quite reach the  
207  $^{210}\text{Pb}$  dating horizon, and the dating model was fitted to the  $^{137}\text{Cs}$  peaks for 1963 and 1986  
208 (Chernobyl). For cores where samples extended beyond the  $^{210}\text{Pb}$  dating horizon, dates were  
209 extrapolated from the lowermost two intervals with measurable excess  $^{210}\text{Pb}$ , 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  $^{137}\text{Cs}$  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<sup>-1</sup> organic matter, where the organic fraction was determined using weight-  
223 loss-on-ignition (LOI) at 550°C (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 ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopes and  
231 elemental % C and N measurements (for C/N ratios) were analysed using a ThermoQuest (F-  
232 MAT) Delta<sup>PLUS</sup>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<sub>2</sub> 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  $\delta^{13}\text{C}$  values of atmospheric CO<sub>2</sub> from the average pre-industrial value  
237 (-6.49‰) for each sample based on its <sup>210</sup>Pb year according to the updated equation in  
238 Verburg (2007).

239

240 *Statistical analysis*

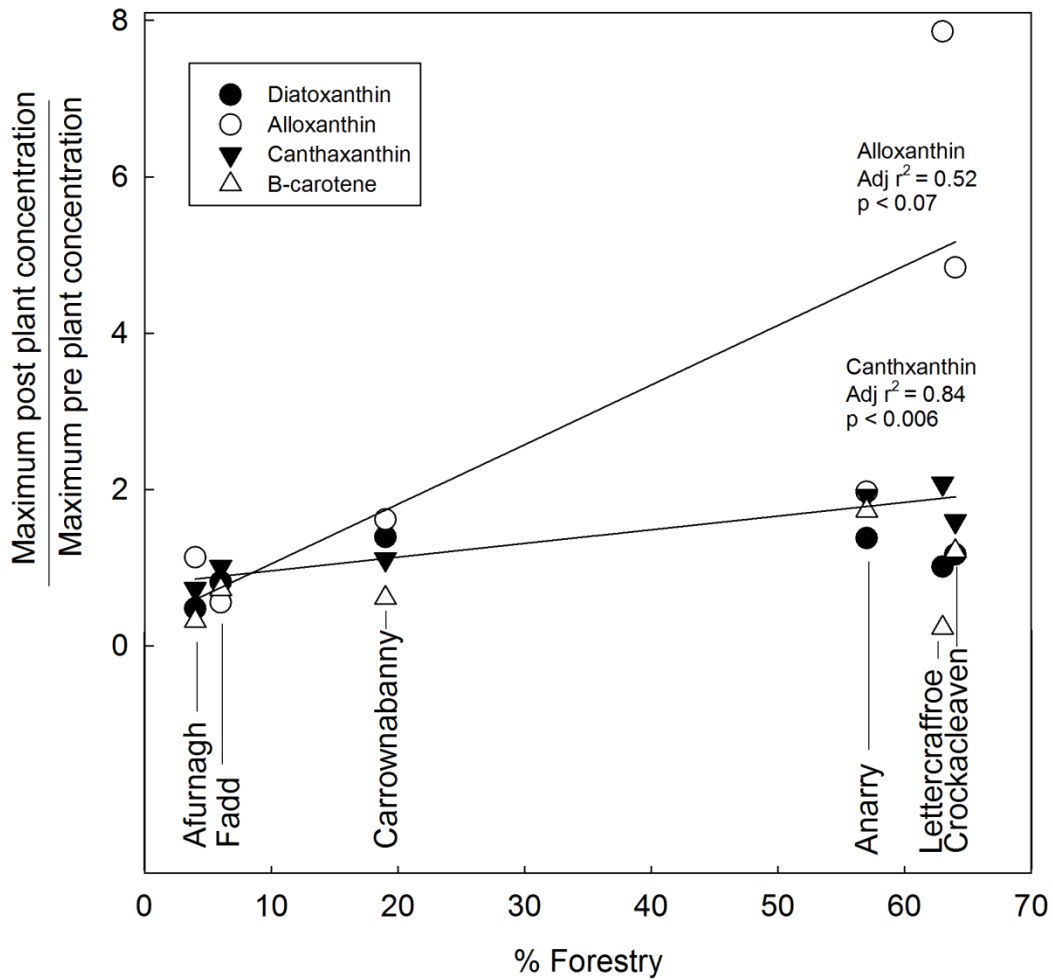
241 Historical changes in gross algal community composition were estimated using  
242 biomarker carotenoids including those from siliceous algae (diatoxanthin), cryptophytes  
243 (alloxanthin), cyanobacteria (canthaxanthin) and all algae ( $\beta$ -carotene). Differences between  
244 mean pigment 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 ( $\beta$ -carotene), carbon and nitrogen stable isotopes ( $\delta^{13}\text{C}$  &  $\delta^{15}\text{N}$ ),  
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 ( $\delta^{15}\text{N}$ ) 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*

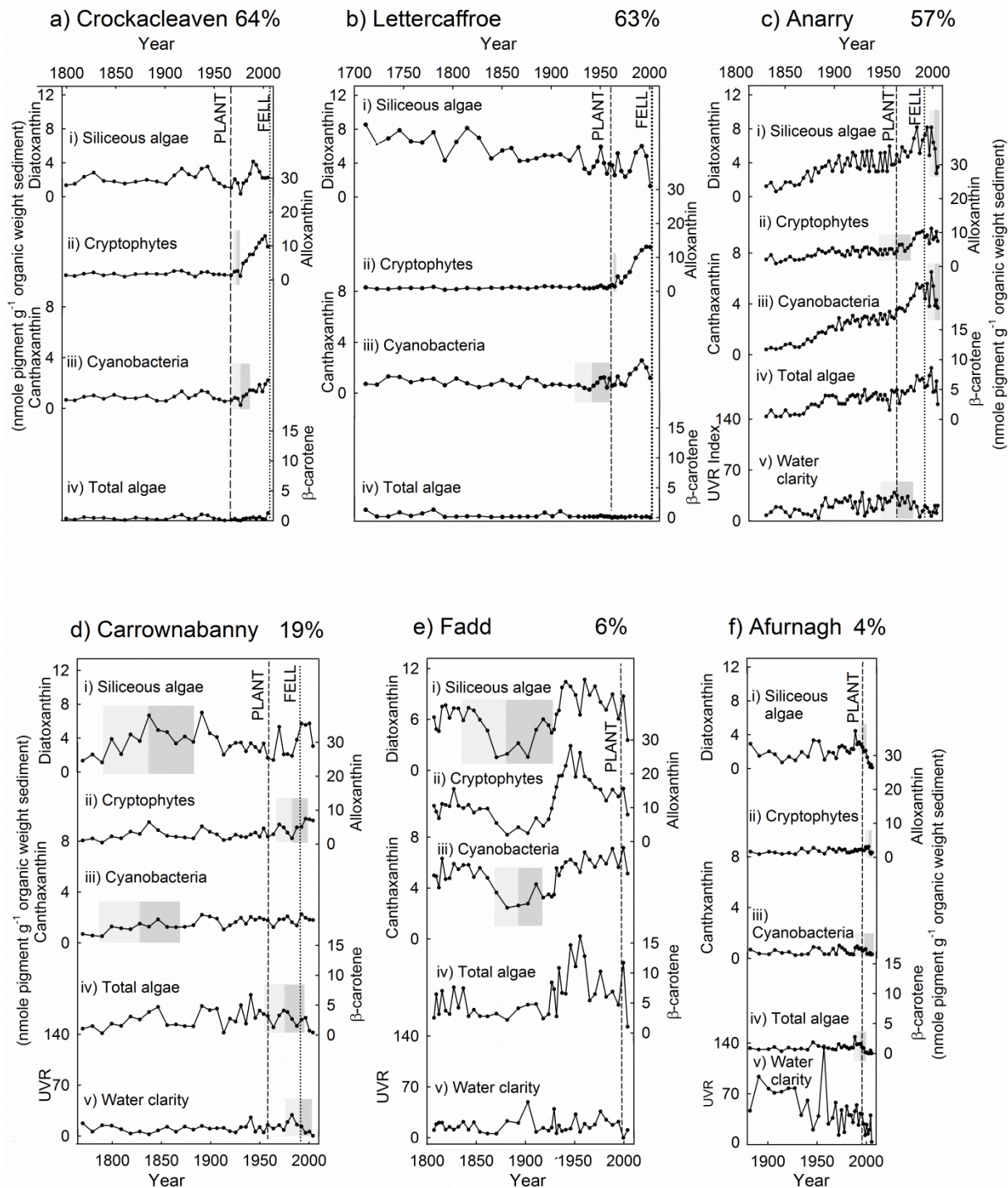
267 Concentrations of sedimentary alloxanthin (cryptophytes) and canthaxanthin  
268 (cyanobacteria) increased significantly in the three lakes with the largest forest cover after  
269 planting; Crockacleaven, Lettercraffroe and Anarry (Fig. 2, 3a-c). There was a six-fold  
270 increase in cryptophyte 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).





278

279 Figure 2: Ratio of maximum post-plant pigment concentration (since first plant) over  
 280 maximum pre-plant (since 1900) pigment concentration against catchment percentage planted  
 281 forestry. Linear regressions are presented for alloxanthin (cryptophytes) and canthaxanthin  
 282 (cyanobacteria) pigments. A similar result was obtained when mean post-plant pigment  
 283 concentration over mean pre-plant pigment concentrations were used (canthaxanthin adjusted  
 284  $r^2 = 0.62$ ,  $p = 0.04$ ; alloxanthin adjusted  $r^2 = 0.49$ ,  $p = 0.07$ ) (S. Figure 1).



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 ( $\beta$ -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 ( $\pm$ SD) and non-parametric Mann–Whitney  $U$  test values before and after afforestation for selected key pigment variables (diatoxanthin, alloxanthin, canthaxanthin and  $\beta$ -carotene).

			Crockacleaven	Lettercraffroe	Anarry	Carrownabanny	Fadd	Afurnagh
First planting			1967	1960	1963	1960	1996	1998
Diatoms (diatoxanthin)	Mean concentration ( $\pm$ SD)	<i>before</i>	2.1 $\pm$ 0.69	5.4 $\pm$ 1.6	3.3 $\pm$ 1.35	3.5 $\pm$ 1.43	6.5 $\pm$ 2.36	2.2 $\pm$ 0.85
		<i>after</i>	2.2 $\pm$ 1.0	3.7 $\pm$ 1.5	5.8 $\pm$ 1.58	3.7 $\pm$ 1.8	6.1 $\pm$ 3.7	1 $\pm$ 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 ( $\pm$ SD)	<i>before</i>	1.7 $\pm$ 0.48	1.0 $\pm$ 0.29	3.8 $\pm$ 1.25	2.6 $\pm$ 1.35	12.5 $\pm$ 6.25	1.8 $\pm$ 0.57
		<i>after</i>	6.8 $\pm$ 4.1	6.8 $\pm$ 4.7	7.9 $\pm$ 2.1	5.0 $\pm$ 1.9	11.8 $\pm$ 5.4	2.1 $\pm$ 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 ( $\pm$ SD)	<i>before</i>	0.89 $\pm$ 0.25	0.80 $\pm$ 0.30	2.08 $\pm$ 0.93	1.47 $\pm$ 0.47	5.02 $\pm$ 1.23	0.56 $\pm$ 0.24
		<i>after</i>	1.24 $\pm$ 0.55	1.3 $\pm$ 0.69	4.50 $\pm$ 0.91	1.78 $\pm$ 0.31	6.14 $\pm$ 1.43	0.45 $\pm$ 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 ( $\beta$ -carotene)	Mean concentration ( $\pm$ SD)	<i>before</i>	0.4 $\pm$ 0.28	0.4 $\pm$ 0.36	2.9 $\pm$ 1.33	2.8 $\pm$ 1.57	6.1 $\pm$ 3.56	1.1 $\pm$ 0.49
		<i>after</i>	0.4 $\pm$ 0.32	0.1 $\pm$ 0.08	5.4 $\pm$ 1.56	2.3 $\pm$ 1.28	6.4 $\pm$ 7.57	0.2 $\pm$ 0.32
	U	113	52	69	108	33	11	
	P	0.548	0.001*	<0.001**	0.454	0.871	<0.001**	
No. samples	<i>before</i>	20	30	18	10	36	7	
	<i>after</i>	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  $\beta$ -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

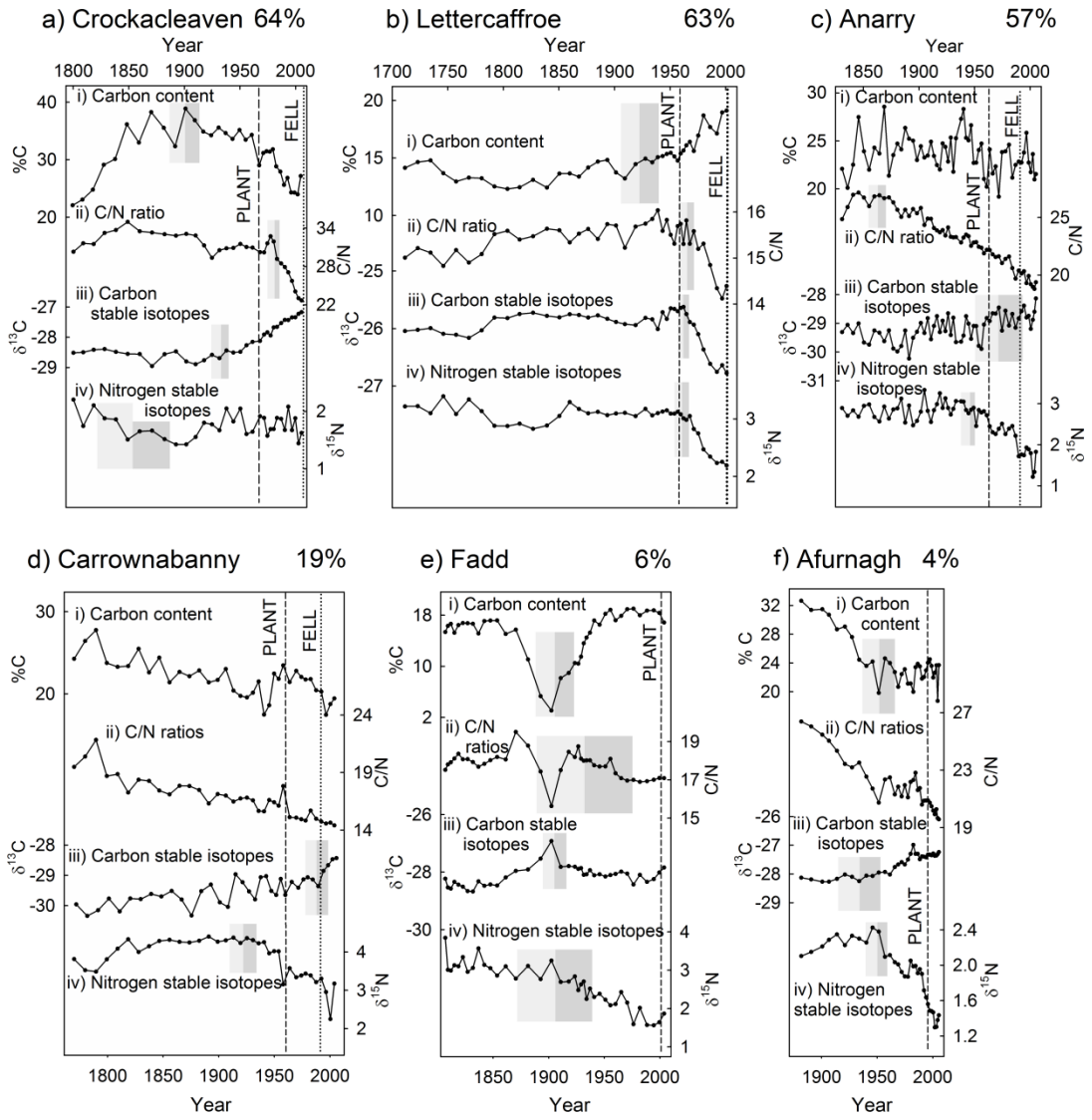
322 indices both before and after forest planting (Fig 3d-f). Unlike the more heavily managed  
323 catchments, fossil alloxanthin or canthaxanthin content exhibited little directional change in  
324 Carrownabanny and planting was too recent in control sites Fadd and Afurnagh to test for the  
325 effect 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  $\beta$ -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 20<sup>th</sup> century (Fig. 3). For example, in Lettercraffroe, there was a  
333 gradual decline in diatoxanthin (diatoms) from ~1700 to ~2000, with pulses of  $\beta$ -carotene  
334 (total algae) throughout the 1700s and ~1900 (Fig 3b). In contrast, Crockacleaven exhibited  
335 contemporaneous peaks of diatoxanthin (mainly diatoms) and  $\beta$ -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)

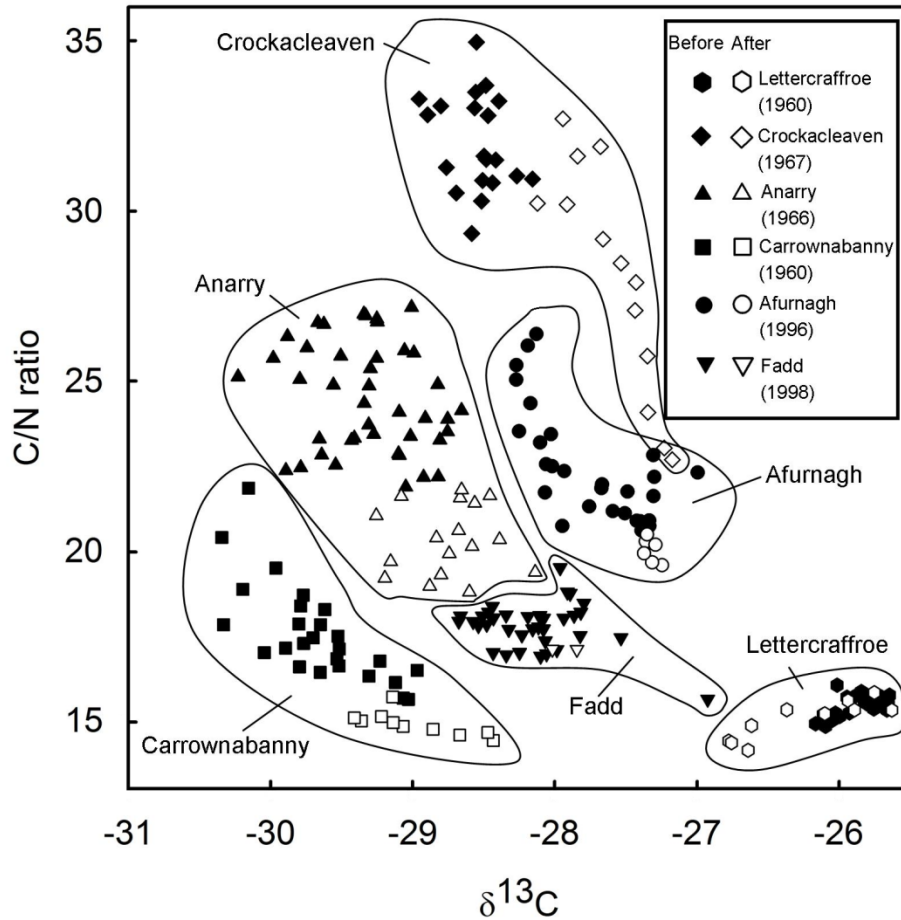
346 (6% afforestation) and declined before planting in Anarry (57% afforestation) and Afurnagh  
347 (4% afforestation) (Fig. 4c, f). In contrast,  $\delta^{13}\text{C}$  values increased in all lakes after plantations  
348 were established, except intensively forested Lettercraffroe where sedimentary carbon  
349 isotopes ratios were sharply depleted after planting (Fig. 4b). At Lettercraffroe breakpoints  
350 for  $\delta^{13}\text{C}$  ratios (1962, 95% CI 1957-1967),  $\delta^{15}\text{N}$  (1961, 95% CI 1954-1967) and C/N ratio  
351 (1965, CI 1958-1971) were all clearly coincident with tree planting (all  $p < 0.001$ ) (Fig. 4b, S.  
352 Table 1). However, in Crockacleaven no breakpoints were perfectly coincident with planting;  
353 rather the breakpoint for C/N was slightly after planting (1980, 95% CI 1974-1985), while in  
354 Anarry only the breakpoint for  $\delta^{13}\text{C}$  was coincident with forestry (1972, 95% CI 1950-1993)  
355 (Fig. 4a,c; S. Table 2). When plotted together (Fig. 5), lake zones defined by C/N ratios and  
356  $\delta^{13}\text{C}$  values revealed that afforestation typically produced changes characteristic of increased  
357 algal production in dilute lakes (lower C/N, enriched  $\delta^{13}\text{C}$ ), with the exception of  
358 Lettercraffroe (lower C/N but depleted  $\delta^{13}\text{C}$  (Fig. 4b)) and Fadd for which there were no  
359 separation of pre and post planting samples.



360  
361



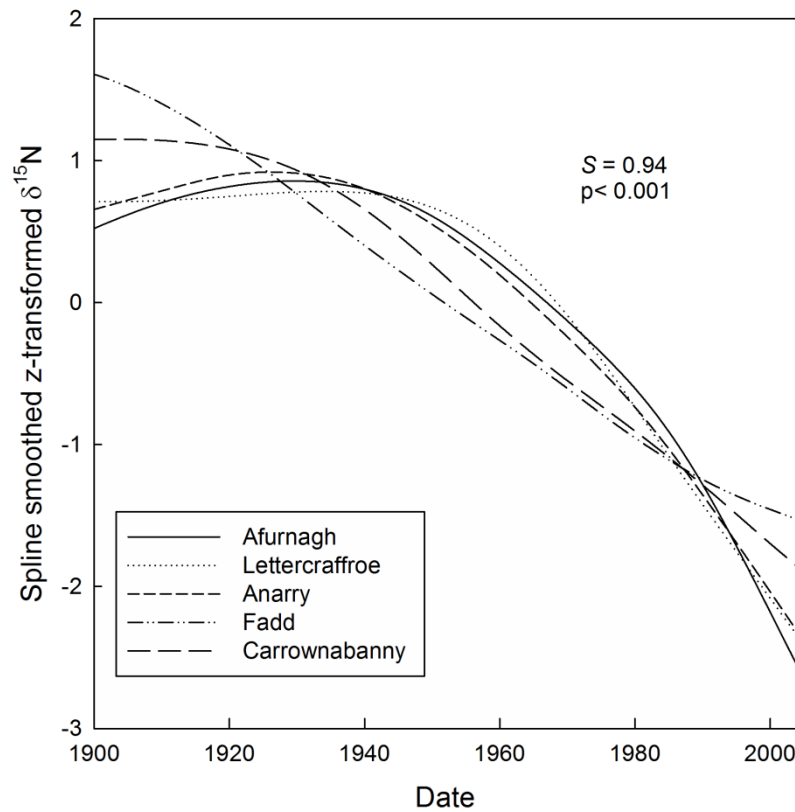
362 Figure 4: Changes in bulk and isotopic measures for (a) Crockacleaven, (b) Lettercraffroe, (c)  
363 Anarry, (d) Carrownabanny, (e) Fadd and (f) Afurnagh. Variables include: (i) carbon content  
364 determined by elemental analysis on bulk carbon (%C), (ii) C/N ratio, (iii)  $\delta^{13}\text{C}$ , and (iv)  $\delta^{15}\text{N}$ .  
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

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

375 Overall, nitrogen isotope values declined during the 20<sup>th</sup> 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,  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  were plotted against  
383 percentage forestry, a clear trend was established between higher planted forestry and  $\delta^{15}\text{N}$   
384 (maximum  $R^2$ -adj = 0.64,  $p <0.03$ ) (S. Fig. 2).



385

386 Figure 6: Synchrony analysis of polynomial spline smoothed nitrogen isotope ( $\delta^{15}\text{N}$ ) data  
 387 interpolated at yearly intervals and Z-transformed against date for Afurnagh, Lettercraffroe,  
 388 Anarry, Fadd and Carrownabanny, with significance established using 999 Monte Carlo  
 389 randomizations. When Crockacleaven was included in the model the results indicated lower,  
 390 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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  values occurred ~1890, followed by a  
400 return to previous levels by ~1940 (Fig. 4e). Similarly, temporal variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
401 values was generally lower in the 19<sup>th</sup> century than during the 20<sup>th</sup> century.

## 402 **Discussion**

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

### 413 *Limnological consequences of intensive conifer plantations*

414           The significant increases in concentrations of fossil canthaxanthin and alloxanthin  
415 after tree planting in Crockacleaven, Lettercraffroe and, to a lesser extent, Anarry catchments  
416 suggest that forest planting was a major factor regulating growth of cryptophytes and  
417 cyanobacteria in these lakes (Fig. 3). Consistent with this interpretation, C/N ratios declined  
418 in these lakes immediately after forest planting indicating that more of the sedimentary  
419 carbon was derived from algal sources (Meyers & Teranes, 2001), while in most cases  $\delta^{13}\text{C}$   
420 values increased <1‰ from depleted values between -28 and -30‰. In most lakes with  
421 enrichment, this meant  $\delta^{13}\text{C}$  isotopes moved to values characteristic of algal respired  $\text{CO}_2$  (ca.  
422 -27‰) (Meyers & Teranes, 2001). However, in Lettercraffroe there was a decline in  $\delta^{13}\text{C}$   
423 after planting as previous values were higher, indicating a switch in algal source (Figure 5).

424           Management of afforested catchments may favour enhanced algal abundance through  
425 runoff of fertilisers. Commercial forestry in ROI and NI has often fertilised soils at rates (50-

426 90 kg P/ha) (Dickson & Savill, 1974) which exceed the P-binding capacity of such iron- and  
427 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  $\beta$ -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

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 Crockacleaveen 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 al.*,  
464 2012) and changes in hydrology associated with the NAO (George *et al.*, 2004, Adrian *et al.*,  
465 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 19<sup>th</sup> 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-19<sup>th</sup> century (as early as the 1860s) (Flower *et al.*, 1994,

499 Aherne & Curtis, 2003, O'Dwyer & Taylor, 2010). Although, Crockacleaveen 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  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  decline is only  
511 coincident with planting in one lake (Lettercraffroe) we do not interpret the broad pattern of  
512  $\delta^{15}\text{N}$  depletion to be driven by catchment land use. Instead, this highly synchronous decline  
513 in  $\delta^{15}\text{N}$  may be related to atmospheric deposition of  $\text{Nr}$  (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  $\text{Nr}$  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  $\text{Nr}$  (Galloway *et al.*, 2008). Regardless of the precise pathway of N influx,

523 synchronous declines in  $\delta^{15}\text{N}$  during the 20<sup>th</sup> 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 brush-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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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).