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Testing the cause of the *Sphagnum austinii* (Sull. ex Aust.) decline: multiproxy evidence from a raised bog in Northern Ireland

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**Keywords**

*Sphagnum austinii; Sphagnum imbricatum; land-use; late Holocene; raised bog; Ireland*
Abstract

We use a multiproxy palaeoecological dataset from Dead Island bog in Northern Ireland to examine the cause of the *Sphagnum austinii* (*Sphagnum imbricatum*) decline. The disappearance of this species from the peat record occurred just after the ‘AD 860’ tephra layer and is coeval with a rapid increase in bog surface wetness and increased mineral dust and charcoal abundance. Although it is difficult to identify one specific cause of the decline, the evidence for increased soil-derived dust is apparent and is supported by regional tephra-dated pollen diagrams that reveal extensive landscape changes due to agricultural intensification in early Medieval Ireland. As the decline of *Sphagnum austinii* occurred much later (~AD 1860) in Fallahogy bog (~1.2 km away), we suggest that the decline of *Sphagnum austinii* at Dead Island was caused by a combination of fire and the deposition of soil-derived dust. We suggest that future studies should consider the use of multiple cores from each site to examine the within-site variability of the decline of *Sphagnum austinii*. 
Introduction

The use of plant macrofossils for investigating ecological change in peatland vegetation and to infer past hydrological conditions is well-established (Barber et al., 1994; Barber et al., 1998; Hughes et al., 2000; Swindles et al., 2007; Mauquoy et al., 2008). The relationship between plant macrofossils and surface wetness is reasonably well understood from the analysis of modern vegetation communities (e.g. Väliranta et al., 2012) and thus hydrological interpretation from plant macrofossil assemblages in peats is firmly based on uniformitarianism (Stoneman et al., 1993). However, a common problem species for peatland palaeoecological research is *Sphagnum austinii* Sull. ex Aust. (formerly *S. imbricatum* Hornsch. Ex Russ.). This moss has been established as an ombrotrophic bog taxon, separate from the fen taxon *Sphagnum affine* (Thingsgaard, 2002), and recognized as a distinct species in the revised bryophyte flora of the British Isles (Smith, 2004).

In the past, *S. austinii* was abundant in many peatlands across the United Kingdom, Ireland and North West Europe, but in the British Isles is now generally confined to only a few sites in Scotland, NW Wales and Ireland. Where this species is still present it is often forms large, dense hummocks (Daniels and Eddy, 1990). The decline of *Sphagnum austinii* is said to represent “the most striking vegetation change on the raised bogs of Britain and Northwest Europe during the last 2000 years” (Hughes et al., 2008: p.1033); however, its contraction of range shows no uniformity either temporally or spatially.

The scarcity of *Sphagnum austinii* in modern peatland vegetation communities causes difficulties when developing quantitative palaeohydrological inferences from fossil plant macrofossil assemblages. This species once formed a great bulk of Holocene peat, but the precise conditions under which it prospered in the past remain an enigma (Green, 1968). At some sites the decline of *S. austinii* occurred over only a few decades, and the main phase of decline is generally between cal. AD 1030-1730 (McClymont et al., 2008). *S. austinii* is often replaced in peat stratigraphy by other
Sphagna including \textit{S. magellanicum}, \textit{S. sect. Cuspidata}, \textit{S. papillosum} or \textit{S. sect. Acutifolia} (van Geel and Middeldorp, 1988; Mauquoy and Barber, 1999). The driving forces behind the decline remain unqualified and greatly disputed with a number of hypotheses put forward, such as:

\textit{(i) Increased bog surface wetness (BSW) and climate change.} At some sites the decline of \textit{S. austinii} is associated with increased mire surface wetness (McClymont et al., 2008; Mauquoy and Barber, 1999). Palaeoecological data from Butterburn Flow in Northern England suggest that a combination of increased BSW and changing aeolian nutrient inputs (see iii) caused the disappearance of \textit{S. austinii} (McClymont et al., 2008). However, evidence from Cars Caron bog in Wales shows that this species has survived similar shifts in BSW in the past, where it declined to trace levels and then regained dominance when the wet phase ended (Hughes et al., 2007). It has been suggested that climate may have driven the increased mire surface wetness leading to the decline of \textit{S. austinii} (e.g. Mauquoy and Barber, 1999). However, the role of climate change in the loss of \textit{S. austinii} has been disputed, since the species has survived well-documented past climatic events. For example, in Raheenmore in Ireland, the species is still present alongside \textit{S. magellanicum}, having re-established itself after the ‘Little Ice Age’ (LIA) (Schulz, 2004). Given earlier discussions on the low genetic diversity of \textit{S. austinii}, it is likely all colonies would react in a similar manner to any broad scale shifts to climate, but this is shown to not be the case (Hughes et al., 2007).

\textit{(ii) Competition.} Other research has suggested interaction and growth competition between species were a driving force in the disappearance of this taxon (Flatberg, 1986). For example, at two sites in Northern England, inter-specific competition, coinciding with shifts in climate have been proposed as the reason for the loss (Mauquoy and Barber, 1999). Conversely, Gunnarson (2005) has suggested that \textit{S. austinii} and \textit{S. magellanicum} are competitively equal as they have the same annual production rates. This would imply inter-specific competition in relation to changing BSW is
negligible (Robroek et al., 2007; 2009). There are differences in the attributes of different *Sphagnum* species (e.g. physiology, limiting factors and tolerances) that lead to variations in their relative resilience to changing environmental factors such as nutrient deposition and hydrological change (Hill et al., 2007). However, there is no evidence in moss attribute data (e.g. Ellenberg indicator values - Ellenberg et al., 1991; Hill et al., 1999) to suggest that other common peatland Sphagna (e.g. *Sphagnum capillifolium, Sphagnum papillosum* and *Sphagnum magellanicum*) have a wider tolerance to environmental factors (light, moisture, pH, Nitrogen, salt tolerance, heavy metal tolerance) than *S. austinii*.

(iii) Changes in nutrient and other atmospheric inputs. With many *Sphagnum* species being extremely sensitive to solute supply (e.g. Lee et al., 1993), changes in nutrients and atmospheric inputs have been suggested as a driving factor in the loss of *S. austinii*. At Carbury Bog in Ireland, an increase in nitrogen levels was proposed as the cause behind the replacement of *S. austinii* by *S. magellanicum* (van Geel and Middeldorp, 1988). This was linked to agricultural intensification in the area surrounding the bog, marked by a decrease in tree pollen, and an increase in atmospheric dust levels. However, the presence of *S. austinii* in a number of Irish bogs where present day atmospheric N deposition is likely to be greater complicates this argument (Robroek et al., 2009). Other studies have discussed major changes in peatland ecosystems driven by inputs of atmospheric dust and tephra (e.g. Ireland and Booth, 2012; Hughes et al., 2013).

(iv) Direct human disturbance on sites. Anthropogenic impact on sites, through burning and drainage, has also been suggested to be one possible reason for the decline of this “sensitive” species (Hill, 1988). *Eriophorum vaginatum* has been shown to temporarily dominate peatland vegetation communities following burning events (Bragg and Tallis, 2001, Holden et al., 2007). Roebroek et al. (2009) suggest that this results in a fluctuating water table, which allows species that
thrive in a wide range of hydrological conditions to rapidly colonise post burning. e.g. *S. magellanicum*. Over the last 2000 years, land-use intensity has increased in areas surrounding peatlands and this is suggested to be linked to the decline of *S. austinii*. In Cors Caron (Wales), and Abbeyknockmoy bog (Ireland), land use changes identified from pollen records provide evidence for the re-establishment of the species in phases of reduced human activity (Hughes et al., 2007; Hughes et al., 2008).

(v) Genetic erosion. *Sphagnum austinii* has been established as a “genetically eroded” (Thingsgaard, 2002: pg. 3) species due to postglacial migration, causing severe genetic bottlenecks caused by a series of founder effects. This loss of genetic diversity has left this species requiring specific conditions of low productivity (in which few other moss species will survive) as well as an oceanic climate providing constant humidity for it to thrive (Thingsgaard, 2002); conditions which few sites now meet.

(vi) Taxonomic error. It has even been theorized that the identification of *S. austinii* in peatland hollow microforms prior to its decline may reflect a misidentification of *S. affine*, due to its co-existence with *S. section Cuspidata* (Thingsgaard, 2002). However, it is generally accepted that any such taxonomic issues cannot account for the decline of this species.

In this paper we attempt to test the cause of the decline of *Sphagnum austinii* in a raised bog in Northern Ireland, using a multiproxy palaeoecological approach. We test the hypothesis that the aerial deposition of soil dust caused the decline of *Sphagnum austinii* as proposed by Hughes et al., (2008).

**Study site**
Dead Island is a lowland raised bog lying in a shallow inter-drumlin hollow within the Lower Bann valley (Fig. 1). The site has a large intact core of deep peat (Fig. 2) with shallow pools and a well-developed hummock and lawn complex. The surface vegetation at Dead Island comprises Calluna vulgaris, Erica tetralix, Eriophorum vaginatum, Eriophorum angustifolium, Scirpus cespitosus, Sphagnum capillifolium and a few isolated hummocks of Sphagnum austini.

Bog pools are dominated by Sphagnum cuspidatum and are often fringed by Sphagnum magellanicum, Sphagnum papillosum and in some places Sphagnum tenellum. Vaccinium oxycoccos is also present in a number of wetter locations. Other plants include Rhynchospora alba, Narthecium ossifragum, Drosera rotundifolia and Cladonia lichens. Mean January and July temperatures at the site are 4-6 and 12-16°C respectively. Mean annual rainfall is between 900-1000 mm and mean annual potential evapotranspiration is between 400-450 mm (Swindles, 2006).

Methods

A core was extracted from a lawn microform on the main bog cupola at Dead Island using a wide-capacity Russian D-section corer with a 50 cm long chamber (Jowsey, 1966; De Vleeschouwer et al., 2010). The cores were wrapped in aluminium foil, returned to the laboratory and stored in refrigeration at 4°C. The core was generally composed of Sphagnum peat with some Calluna and Eriophorum and occasional pool-mud horizons. Testate amoebae were extracted from the samples using a modified version of the method described by Hendon and Charman (1997) as deionised water was used as a storage medium and mountant rather than glycerol. Testate amoebae were identified using Charman et al. (2000). Peatland water table reconstructions were carried out using the ACCROTELM pan-European and North of Ireland transfer functions (Charman et al., 2007; Swindles et al., 2009). Humification and plant macrofossil analyses were undertaken following Roos-Barraclough (2004) and Barber et al. (1994). Plant macrofossils were identified using Grosse-
Brauckmann (1972, 1974, 1992) and Katz et al. (1977). Loss-on-ignition analysis was carried out following Schulte and Hopkins (1996) to evaluate aeolian inputs to the peatland. The resulting ashes from loss-on-ignition were washed in a 10 µm mesh and mounted on slides using Histomount. The abundance of quartz grains were estimated on an ordinal 0-5 scale (where 0 signifies absence and 5 is very abundant). Macro-charcoal particles were also counted in the plant macrofossil samples and evaluated on the same scale. The Dead Island core chronology is based on tephrochronology, AMS $^{14}$C dating and spheroidal carbonaceous particles as fully described in Swindles et al. (2010a, 2012). The cryptotephras were extracted following Swindles et al. (2010b) and analysed by electron microprobe microanalysis at Edinburgh and Leeds Universities (Fig. 3).

**Results and discussion**

The decline of *Sphagnum austini*i at Dead Island occurred just after the AD 860 tephra layer and before the Hekla 1104 tephra layer (Figs 4 and 5), and is thus dated to c. AD 980. It is replaced by *Sphagnum magellanicum* and *Sphagnum papillosum*. The decline occurred at a time of increased bog surface wetness, reduced loss-on-ignition values, increased quartz abundance as well as a peak in macro-charcoal. Tephra-linked pollen data from nearby sites in the Lower Bann Valley are shown in Fig. 1 and show a phase of major human impact on the landscape centred on the AD 860 tephra. This phase is characterised by a decrease in arboreal pollen percentages (*Alnus, Betula, Corylus*-type and *Quercus*) suggesting scrub and woodland clearance in the Lower Bann Valley (Fig. 6). An increase in grasses (*Poaceae*), sedges (*Cyperaceae*) and agricultural taxa (*Cerealia*-type, *Secale*-type) is observed. The presence of *Secale*-type (rye) and *Linum* (flax) pollen may suggest increasing arable activity close to this site (Hall et al., 1993). This implies that the increased aeolian soil dust in Dead Island at this time (causing the increased quartz and lower loss-on-ignition results) was due to widespread landscape clearance and agricultural intensification across the Bann Valley. The topographic setting of Dead Island may have accentuated the aeolian inputs as the drumlins
surrounding the site would have offered better-drained land suitable for cultivation. A slower peat accumulation rate in the last millennium at Dead Island has been noted (e.g. Swindles et al., 2012). However, the decline of *S. austinii* and the coeval rise of quartz occurred before the onset of this slowdown of peat accumulation (Supplementary material 2). The changes in the pollen data at the same time (Fig. 6) suggest that the increase in quartz is the product of soil erosion by wind resulting from landscape clearance in the Lower Bann Valley rather than due to any changes in peat-accumulation dynamics. A sample of the dust from the peat at the horizon containing the *S. austinii* decline was extracted and subjected to x-ray diffraction (XRD) analysis alongside nine soil samples from around Dead Island (Swindles, 2006). The XRD analysis shows that the dust does not contain any minerals that would indicate anything other than a local provenance (Swindles, 2006; Supplementary material 3).

The abundance of *Sphagnum austinii* in the complete sequence is correlated (using Spearman’s rank) with quartz abundance ($r_s=-0.471$, $p<0.01$), charcoal ($r_s=-0.363$, $p<0.01$) and loss-on-ignition ($r_s=0.288$, $p<0.05$) (Table 1). There is no significant relationship between the abundance of *Sphagnum austinii* and the testate amoeba-derived water table reconstructions. Non-metric multidimensional scaling (NMDS) and redundancy analysis (RDA) show that *S. austinii* plots where loss-on-ignition is high and quartz and charcoal abundance is low, suggesting that these are important factors in determining the success of this species (Fig. 7).

The disappearance of *Sphagnum austinii* is a major feature of peat stratigraphy across the British Isles (e.g. Mauquoy and Barber, 1999; Hughes et al., 2008) that generally occurred within the past 2,000 years, although dates of the decline are highly variable (Hughes et al., 2000; Barber et al., 2003; Langdon and Barber, 2005; Fig. 7, Table 2). The decline has been linked in previous studies to aerial deposition of soil dust in Cors Caron, Wales and Carbury and Abbeyknockmoy bogs, Ireland (van Geel and Middeldorp, 1988; Hughes et al., 2008). Furthermore, at a site in northern England,
Malham Tarn Moss, the very early disappearance of *S. austinii* at c. AD 26 coincides with increased Ti, Y and Rb suggesting soil dust loading of the bog surface (Turner et al., 2014) The pollen record at this site indicates a reduction in arboreal taxa, replaced by increasing proportions of Cyperaceae, Poaceae and *Plantago* sp. pollen. The deposition of soil-derived dust on a peatland surface may be detrimental to *Sphagnum austinii* (e.g. Farmer, 1993) or the deposition of N may benefit competitors including other Sphagna (Lee et al., 1993).

The United Nation Economic Commission for Europe state a critical N load of 5-10 kg N ha⁻¹ y⁻¹ for raised and blanket bogs (APIS, 2012), leading Hughes et al., (2008) to suggest a critical N deposition threshold of <10 kg N ha⁻¹ y⁻¹ for the current day presence of *Sphagnum austinii* in raised bogs across the British Isles. However, the average total N deposition at Dead Island bog in the recent past (2004-2011) was 11.31 kg N ha⁻¹ y⁻¹, with a maximum of 13.84 kg N ha⁻¹ y⁻¹ in 2011 (Defra). This would suggest that *S. austinii* may be able to tolerate higher concentrations of N that previously stated. It could be argued that the ecological effects of N loading are yet to be realised; however, atmospheric N deposition has been in decline over the last three decades (Fowler et al., 2005) thus it can be concluded that this is unlikely. Clearly, the past and current presence of *S. austinii* at Dead Island have been driven by other factors. It is possible that the combination of burning (as there is an increase in charcoal at the time of the decline) and deposition of soil dust caused the decline of *S. austinii* at Dead Island. In Fallahogy raised bog, which is ~1.2 km to the north of Dead Island, there is a subfossil presence of *S. austinii* until ~ AD1860 (Rea, 2011). This much later date of the decline suggests that site-specific factors, such as burning, must have been important.

A recent study found that there is significant within-site variability of subfossil pollen and macrofossil records in a peatland in the Netherlands (Blaauw and Mauquoy, 2012). The presence of *Sphagnum austinii* in hummocks on the present surface of both Dead Island and Fallahogy suggests that the
The cause of the decline of *Sphagnum austinii* may never be fully understood, but the importance of this event in peat-based palaeoenvironmental studies will lead to research into this topic for many years to come. The use and study of contemporary and subfossil plant DNA may have important implications for linking the modern and fossil specimens of this species and understanding its palaeoecology and phylogeography (e.g. Szövényi et al., 2006; Suyama et al., 2008). This may offer further insights into why *Sphagnum austinii* suffered such a dramatic loss in the peatlands of Britain and Ireland.

**Conclusions**

1. A multiproxy palaeoecological dataset from Dead Island raised bog, Northern Ireland is used to examine the cause of the decline of *Sphagnum austinii* (*Sphagnum imbricatum*).

2. The decline of *Sphagnum austinii* in Dead Island bog occurred just after the ‘AD 860’ tephra layer and is coincident with a water table rise, increased mineral dust and charcoal.

3. Significant correlations are found between the abundance of *Sphagnum austinii* and charcoal, loss on ignition and quartz abundance. There is no significant correlations between the abundance of *Sphagnum austinii* and a testate amoebae-based water table reconstruction.

4. Although it is difficult to identity one clear cause of the decline, the results suggest that increased soil-derived dust may have been an important factor, corroborating results from elsewhere in the British Isles. However, the diachronous nature of the decline in two
proximal sites suggest that site-specific factors may be important. The increase in charcoal at Dead Island may suggest that fire was an important factor.

5. Future studies should consider within-site as well as between-site variability in the timing and nature of the decline of *Sphagnum austinii*.

**Acknowledgements**

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**Figure captions**

Figure 1. Aerial photo of Dead Island bog (RAF, 1955) and map showing the location of study sites. The location of the core analysed here is shown on the aerial photo.

Figure 2. Stratigraphy of Dead Island bog (N-S transect).

Figure 3. Ternary diagram of tephra geochemistry from Dead Island (major element oxides as determined by EPMA). Geochemical data is provided in Swindles et al. (2010a).

Figure 4. Multiproxy palaeoenvironmental dataset from Dead Island for the top 1 m (plant macrofossils, testate amoebae and peat properties. Water table reconstructions are based on the Northern Ireland (Swindles et al., 2008) and European (Charman et al., 2007) transfer functions. The positions of the tephra layers are shown. Charcoal and quartz grains are expressed on a relative abundance scale. The prehistoric tephras have been dated to 755-680 cal. BC for OMH-185, 800-758 cal. BC for GB4-150 and 2395-2279 cal. BC for Hekla 4 (Pilcher et al., 1995; Plunkett et al., 2004).
Figure 5. Multiproxy palaeoenvironmental dataset from Dead Island for the complete sequence (plant macrofossils, testate amoebae and peat properties). Water table reconstructions are based on the Northern Ireland (Swindles et al., 2009) and European (Charman et al., 2007) transfer functions. The positions of the tephra layers are shown. Charcoal and quartz grains are expressed on a relative abundance scale. The prehistoric tephras have been dated to 755-680 cal. BC for OMH-185, 800-758 cal. BC for GB4-150 and 2395-2279 cal. BC for Hekla 4 (Pilcher et al., 1995; Plunkett et al., 2004).

Figure 6. Tephra linked pollen diagrams from the Bann Valley: (a) Fallahogy; (b) Ballyscullion East (after Hall et al., 1993, data is from the Global Pollen Database - http://www.ncdc.noaa.gov/paleo/pollen.html). The AD860 and Hekla 1104 tephra layers are shown (grey screens). The phases of decreased arboreal pollen reflecting widespread landscape clearances are highlighted by pink boxes.

Figure 7. NMDS and RDA analysis of the plant macrofossil data. Peat properties and water table reconstructions were included as environmental variables in the RDA. The Bray-Curtis distance was used in NMDS and the samples were classified based on the ordinal scores of quartz (1-5; see data in Figures 4 and 5). Taxon data were Hellinger-transformed prior to RDA analysis. Sphagnum austinii is abbreviated as ‘SA’ (full names for the other taxa can be found in Figures 4 and 5).

Figure 8. Histogram showing the dates of the decline of Sphagnum austinii in Britain and Ireland. The red line is a kernel density function, the black line is the normal distribution.

Table 1. Spearman’s correlation coefficients showing the relationships between % Sphagnum austinii and other down-core variables.
Table 2. Comparison of the dates of decline of *Sphagnum austinii* in peatlands of Britain and Ireland.

Supplementary file 1. Attributes of common peatland Sphagna from Bryoatt tables (Hill et al., 2007).

Supplementary file 2. Bacon age-depth model for Dead Island (for full details see Swindles et al. (2014).

Supplementary file 3. x-ray diffractogram for a Dead Island peat sample (38-43 cm) and nine local soils.

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Figure 1
Figure 3
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Figure 8
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<td>26</td>
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<td>Blundell and Barber (2005)</td>
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</table>
Highlights

- We examine the cause of the *Sphagnum austinii* decline in a raised bog.
- The decline occurs at a time of increased soil-derived dust and increased charcoal.
- Pollen records reveal that the decline occurred during a period of agricultural intensification.