



# Macroinvertebrate community assembly in pools created during peatland restoration



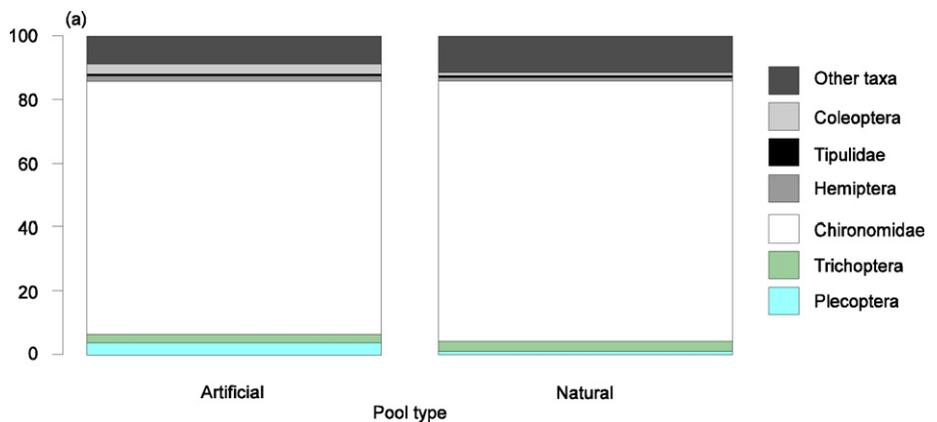
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## HIGHLIGHTS

- We assessed the benefits of peatland pool restoration for aquatic biodiversity.
- Biomonitoring metrics and community composition suggested different outcomes to restoration.
- Null model approaches provided a clearer suggestion that restoration was successful.
- Analysis of assembly processes should be used when planning and evaluating ecological restorations.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Many degraded ecosystems are subject to restoration attempts, providing new opportunities to unravel the processes of ecological community assembly. Restoration of previously drained northern peatlands, primarily to promote peat and carbon accumulation, has created hundreds of thousands of new open water pools. We assessed the potential benefits of this wetland restoration for aquatic biodiversity, and how communities reassemble, by comparing pool ecosystems in regions of the UK Pennines on intact (never drained) versus restored (blocked drainage-ditches) peatland. We also evaluated the conceptual idea that comparing reference ecosystems in terms of their compositional similarity to null assemblages (and thus the relative importance of stochastic versus deterministic assembly) can guide evaluations of restoration success better than analyses of community composition or diversity. Community composition data highlighted some differences in the macroinvertebrate composition of restored pools compared to undisturbed peatland pools, which could be used to suggest that alternative end-points to restoration were influenced by stochastic processes. However, widely used diversity metrics indicated no differences between undisturbed and restored pools. Novel evaluations of restoration using null models confirmed the similarity of deterministic assembly processes from the national species pool across all pools. Stochastic elements were important drivers of between-pool differences at the regional-scale but the scale of these effects was also similar across most of the pools studied. The amalgamation of assembly theory into ecosystem restoration monitoring allows us to conclude with more certainty that restoration has been successful from an ecological perspective in these systems. Evaluation of these UK findings compared to those from peatlands across

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Europe and North America further suggests that restoring peatland pools delivers significant benefits for aquatic fauna by providing extensive new habitat that is largely equivalent to natural pools. More generally, we suggest that assembly theory could provide new benchmarks for planning and evaluating ecological restoration success.

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## 1. Introduction

Degraded, damaged or destroyed ecosystems are the subject of ever increasing attempts to effect restoration of ecological processes, conserve biodiversity and sustain the livelihoods of people who depend upon them (Allison, 2012). Billions of dollars are spent annually on ecosystem restoration (Goldstein et al., 2008; Birch et al., 2010), with estimates for the U.S. alone running to \$9.5B per annum (BenDor et al., 2015). Restoration efforts can include the removal of barriers to recovery, reconfiguration of habitats, or assistance with species recolonization. Biodiversity increases are often cited as a key goal of restoration (Kirkman et al., 2013). However, only 35–44% of restoration programmes across a wide range of ecosystem types have been reported as having favourable outcomes for biodiversity (Benayas et al., 2009; Jones and Schmitz, 2009) leading to the often repeated conclusion that many ecological restoration attempts have been unsuccessful (Lockwood and Pimm, 1999).

A typical focus of ecosystem restoration monitoring is the assessment of empirically measurable attributes of a community such as diversity and abundance (Seabloom and Valk, 2003; Klimkowska et al., 2007; Palmer et al., 2010), biomonitoring index scores (Bonada et al., 2006), indicator species abundance (Pykälä, 2003; González et al., 2013) or aspects of ecosystem functioning (Lepori et al., 2005; Foster et al., 2007) relative to control or reference sites. A potential reason for the reported low success rates, and often unexpected results of ecological restoration, is that structural and functional attributes of ecosystems can reach alternative states as post-restoration succession proceeds (Suding et al., 2004; Hobbs, 2007). Significant drivers of changes in ecosystem structure and functioning include dispersal and colonisation success, biotic interactions and feedbacks which can introduce significant stochasticity to community composition (Ledger et al., 2006; Chase, 2007; Heino et al., 2015) and thus to restoration outcomes. However, incorporating knowledge of reference-community assembly processes in the planning or evaluation of restoration programmes has still not begun (Lockwood and Pimm, 1999; Chase, 2007).

Where environmental conditions do not impose excessively strong controls on biodiversity, there is often a distribution of potential restoration end points which arises rather than a single definable end point (Chase, 2007; Milner et al., 2011). In conceptual terms, evaluating restoration success based on a system's ability to assemble towards this range of states should be desired by practitioners where it is also the case in their reference system(s). However, a general focus by restoration practitioners on restoring abiotic habitat to deliver quite specific biodiversity outcomes means that deterministic (niche) processes of community assembly (Belyea and Lancaster, 1999) are essentially a major consideration within restoration design. In these cases, restoration is only likely to be deemed completely successful where it is aimed at ecosystems that already have strong deterministic assembly processes which serve to 'filter' (Poff, 1997; Fattorini and Halle, 2004) the species pool towards a narrowly defined end point, similar to the reference state.

In environments such as wetlands, which have been degraded historically via land drainage activities, heterogeneity may be decreased following rewetting which aims to homogenise water-table variations and vegetation across a site (Verberk et al., 2010). In such ecosystems, restoration activities provide ideal opportunities to evaluate biological community assembly processes because environmental homogeneity should promote high similarity between the biota of restored environments and local reference sites, especially if environmental conditions are harsh enough to serve as deterministic influences on community assembly (Thompson and Townsend, 2006; Brown and Milner, 2012). In

contrast, if stochastic dispersal events or internal dynamics are important drivers of assembly (Belyea and Lancaster, 1999; Heino, 2012), communities in restored wetland sites might not fully resemble those in reference sites even if environmental conditions show no difference.

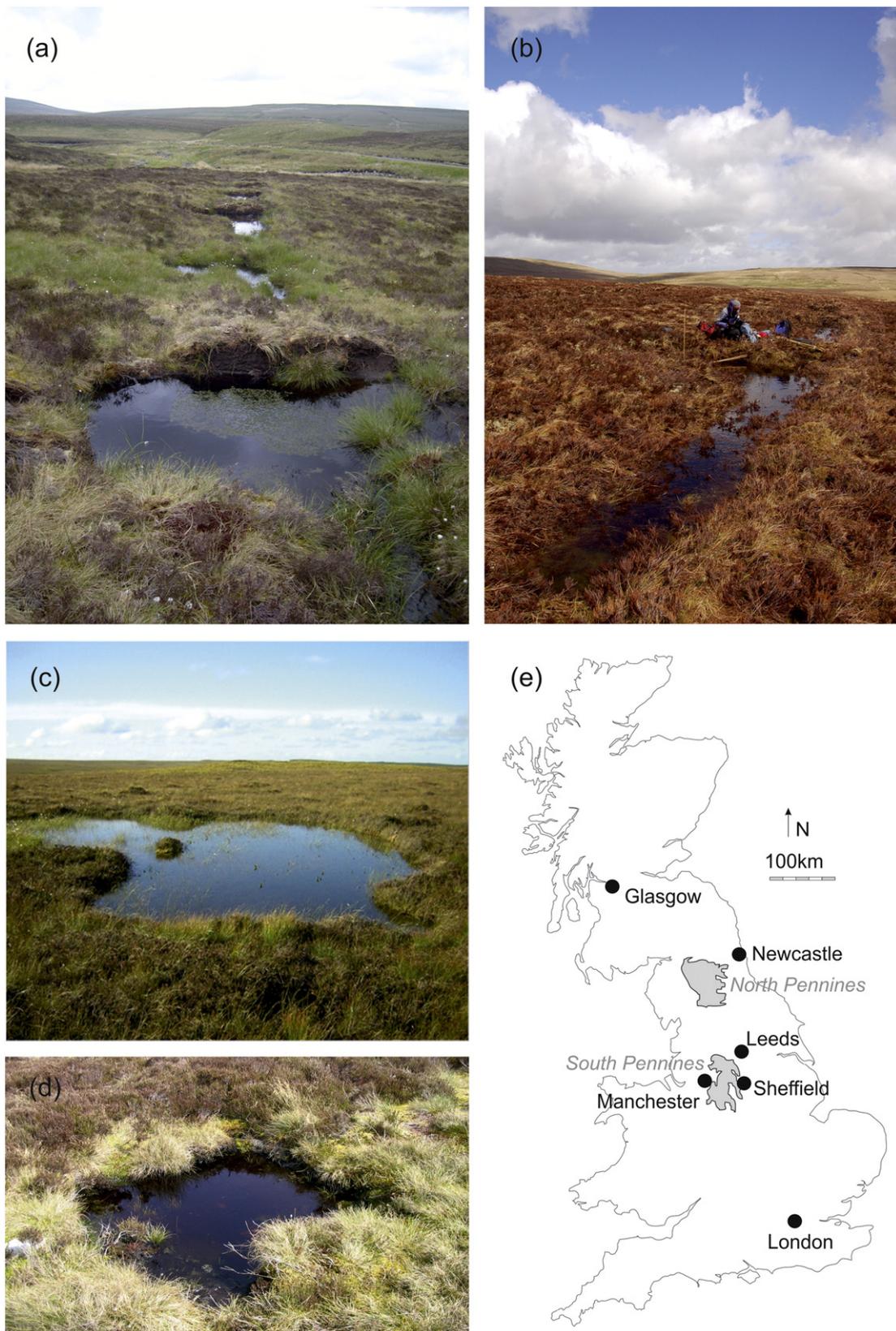
Peatlands cover ~4 M km<sup>2</sup> of northern temperate and boreal regions (Yu, 2012) and large expanses of N. Europe, N. America and Russia have been impacted by land drainage (Holden et al., 2004; Mazerolle et al., 2006; Hannigan et al., 2011; Beadle et al., 2015). Recognition of the global environmental implications of peatland degradation has led to attempts to rewet drained peatlands, with the aim of restoring the growth of peat-forming vegetation, promoting peat accumulation and thus enhancing terrestrial carbon sinks (Poulin et al., 2004; Ramchunder et al., 2009). UK blanket peatlands (Fig. 1) have historically been subjected to intensive drainage to lower the water table in attempts to make the land more suitable for agriculture, gun-sports, commercial forestry or for peat extraction for use as fuel or in horticulture (Holden et al., 2007). Large-scale restoration practices have created hundreds of thousands of open water pools, ponds and lakes (Beadle et al., 2015) but to date they have received relatively little attention with respect to their biodiversity and/or community (re-) assembly compared with studies of their hydrology, chemistry and gas emissions (Haapalehto et al., 2011). Despite the potential importance of new bog pools for aquatic biodiversity, these habitat features are also potential hotspots for the release of both CH<sub>4</sub> and CO<sub>2</sub> (Cliché-Trudeau et al., 2012). This is important because some consideration is being given to infilling ditches, rather than creating pools, to reduce greenhouse gas releases (Parry et al., 2014). It is therefore vital that the biodiversity of these habitats is studied to provide a balanced research base that can inform future management and conservation decisions.

This study investigated the physicochemical characteristics and macroinvertebrate communities of natural versus artificial pools ecosystems, with the aim of first providing a comparative evaluation of their macroinvertebrate community composition. Specifically, we sought to answer the question: do restored pool environments support assemblages similar to naturally formed pools? Second, the integration of ecological theory with practice has been a long-standing goal of restoration (Temperton et al., 2004; Hobbs, 2007), and here we evaluate the benefits of such an approach to assess restoration success alongside widely used measures of community composition and diversity metrics. Third, we evaluated whether or not these pool systems contain biota similar to pools on restored peatlands elsewhere in the northern hemisphere, to shed light on the potential to generalise our findings of deterministic versus stochastic constraints on peatland pool macroinvertebrate communities.

## 2. Methods

### 2.1. Study sites

The study examined 40 independent bog pools (20 natural, 20 artificial) on three occasions in the Pennines of northern England, UK. Potential sites with pools were identified using aerial images available online. All shortlisted sites were visited to ground-truth the management techniques and pool size. The final selection of study sites was determined by selecting restored sites with similar lengths of time for colonisation since peatland restoration had occurred (5–10 years), and where restored peatlands could be compared to nearby intact peatlands with no history of artificial drainage management. Of the 40 pools selected for study, 20 were located in the North Pennines region and 20 in the South Pennines (10 pools on undisturbed peatland vs 10 pools



**Fig. 1.** Photographs of pools located on blanket peatland in the UK uplands: (a) and (b) series of pools created artificially during peatland restoration by the blocking of a drain which runs away from the foreground, (c) and (d) naturally formed pools (width ~1.5 m to 2 m), (e) map of study locations in the North and South Pennines regions of the UK.

on restored peatland in each region). Pools were all typically up to 2–3 m<sup>2</sup> surface area (Fig. 1). The South Pennines region experienced historically higher levels of airborne pollutant deposition from the nearby urban centres of Sheffield and Manchester, whereas the

North Pennines are relatively remote from large urban areas (Caporn and Bridget, 2008); therefore, the study design also allowed us to incorporate a consideration of any legacy effects on pool ecosystem assembly.

In the north, pools were located within the North Pennines AONB including parts of Upper Teesdale and Geltsdale. Artificially-created peatland pools on restored peatland were located at Herdship Fell (54°41'N, 2°21'W) and Middle Top Fell (54°53'N, 2°36'W). Naturally-formed pools were located across Moor House National Nature Reserve (54°41'N, 2°23'W). In the South Pennines, study pools were located in the Dark Peak area. Here artificially-formed pools formed at Winscar (53°30'N, 1°47'W) were contrasted with naturally-formed pools on Midhope Moor (53°28'N, 1°43'W). There were no naturally-formed pools available to sample on the restored peatlands owing to previous drainage activities, therefore the study was designed to make comparisons with the nearest available peatlands that housed natural pools. Artificial pools were selected randomly across the restored peatlands and we avoided sampling pools located on the same former drainage channels to prevent non-independence of pool physicochemical and biotic observations. No pre-restoration sampling was undertaken because there were no pools on the drained peatlands prior to drain-blocking. Pools were sampled in Sept. 2011, March 2012 and June 2012. Sampling was also planned during Dec. 2011 but was not possible as all of the pools were frozen at the surface.

All sites had blanket peat cover, with vegetation dominated by *Eriophorum* spp. and *Calluna vulgaris* (L.). There was *Sphagnum* spp. cover at all sites, but this was less abundant in the South Pennines. Contextual meteorological data were not available for all sites but, for example, mean annual precipitation of 2012 mm (1951–1980; 1991–2006) occurs at Moor House (Holden and Rose, 2011) and 1123 mm (1961–1990) at Geltsdale reserve, North Pennines (Jonczyk et al., 2009), and from 1000 to 1584 mm across the South Pennines (Evans and Jenkins, 2000). Mean annual air temperature at Moor House is 5.3 °C (1931–2006 (Holden and Rose, 2011)) and in the South Pennines mean monthly temperatures range from 2 to 14 °C (Evans and Jenkins, 2000).

## 2.2. Field sampling

At each pool on each sampling date, nine environmental variables were measured to contrast physicochemical habitat between pool types. Measurements of physicochemical variables that are key influences on aquatic macroinvertebrates focused on water temperature, pH, dissolved oxygen (DO) and turbidity. A Hach Lange (Salford, UK) HQ30d handheld probe was used for the first three measurements, and turbidity was measured using a Hanna Instruments 93,703 turbidity meter. At each pool, average depth was calculated from seven random measurements. Additionally, 50 mL of water was passed through a 0.45 µm filter and subsequently analysed for key nutrients (NO<sub>3</sub>, dissolved organic carbon (DOC)) and metals (inorganic Al, Fe) that can influence the abundance of some sensitive invertebrate taxa (Brown et al.,

2013). DOC was measured with a Thermalox 8000 total carbon analyser (Metrohm UK, Ltd., Buckingham, UK), NO<sub>3</sub> with a Dionex 4000i chromatograph in conjunction with an automatic sampler, and Al and Fe using an Optima 5300DV instrument (PerkinElmer, Massachusetts, US).

Macroinvertebrates were selected as a 'model' biological group to evaluate restoration success because they are ubiquitous in aquatic environments, easy to collect and identify, they exhibit a range of responses to differences in environmental conditions, and dispersal ability varies between groups. Macroinvertebrate samples were collected using a long handled net (250 µm mesh). A total of three minute sampling was undertaken, with 2 min of sampling time divided equally between observed mesohabitats (i.e. open water, vegetation, pool bottom) and an additional 1 min spent searching for pleustonic animals (Nicolet et al., 2004). Samples were preserved in 70% methylated spirits then, after sorting in the laboratory, macroinvertebrates were identified to species level (where possible) under a light microscope (up to ×40 magnification) using standard keys (Pawley et al., 2011 and references therein). Whilst identification at mixed levels of taxonomy might have modified the summary metrics and community analyses we generated, there was necessarily a trade-off between identifying the most abundant groups such as Chironomidae to species level to maximise the ability to discriminate between samples (Jones, 2008), versus coarser identification of less common taxa for which larval identification beyond Family is difficult (e.g. other Diptera). Chironomidae were subsampled (n = 50) where abundance per sample was >50 individuals. Individuals were cleared in 10% KOH, transferred to 99.85% glacial acetic acid for 5 min, rinsed in ethanol and then mounted on slides using Euparal. Chironomidae were identified using Rieradevall and Brooks (2001) and Brooks et al. (2007).

## 2.3. Data analysis

Non-metric multidimensional scaling (NMDS) was used to investigate how community composition (based on square-root transformed abundance data) varied between region, pool type and between sampling dates, using the Vegan package (Oksanen, 2005) in R. Bray-Curtis dissimilarities were used and the best two-dimensional solution retained following up to 200 restarts. Physicochemical variable vectors were fitted to the solution post-hoc using the envfit procedure with 999 permutations. This approach was preferred over direct ordination approaches such as RDA/CCA because NMDS makes no assumptions about the underlying data structure, and better represents the distances between samples in ordination space (Legendre and Legendre, 1998). PERMANOVA was undertaken using the Vegan package (Oksanen, 2005) in R2.14.0 (R Development Core Team, 2014) to determine

**Table 1**  
Descriptive statistics and GLMM results for undisturbed and restored peatland pool physicochemical variables.

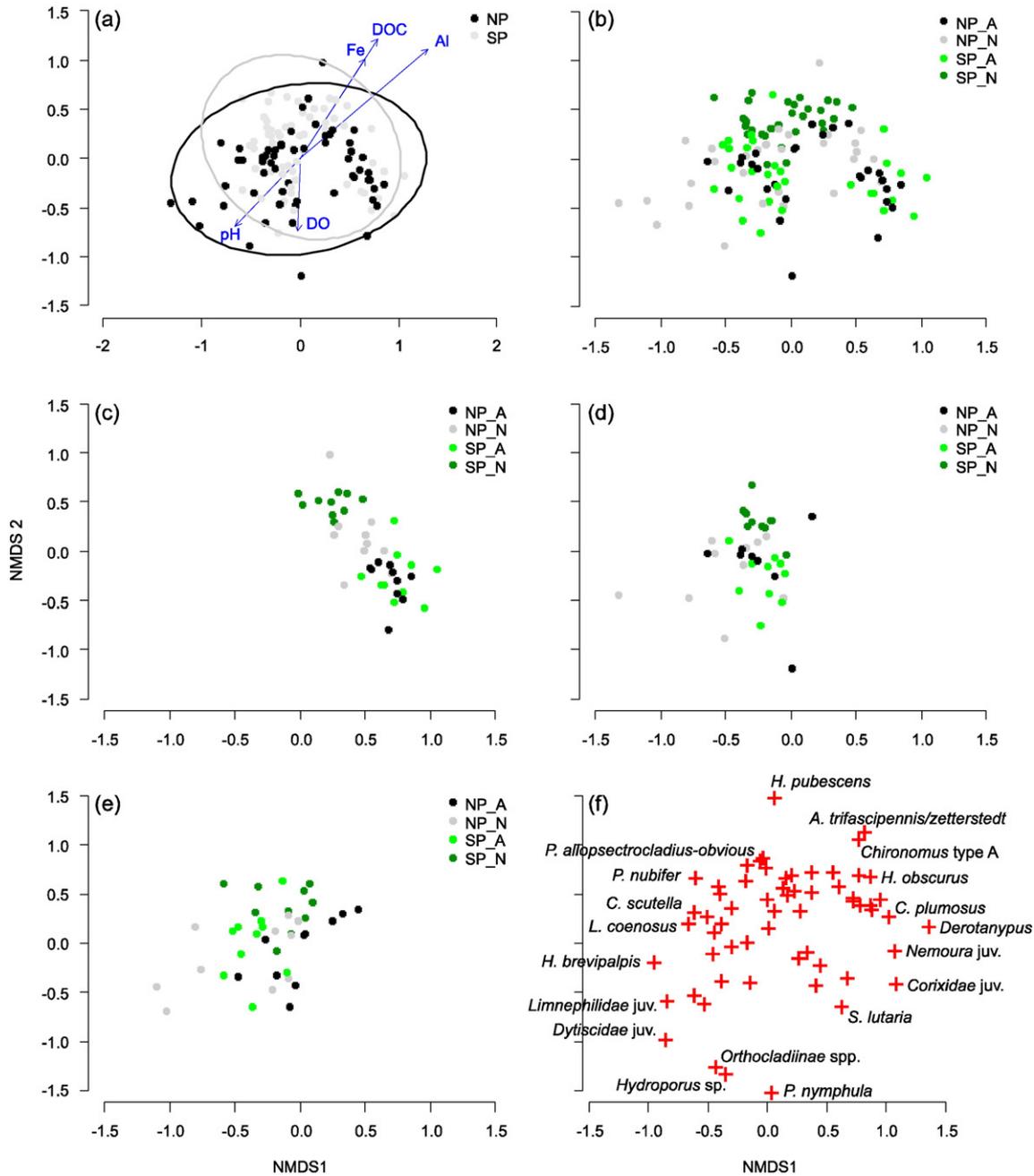
	NO <sub>3</sub> (mg L <sup>-1</sup> )	Al (mg L <sup>-1</sup> )	Fe (mg L <sup>-1</sup> )	DOC (mg L <sup>-1</sup> )	DO (mg L <sup>-1</sup> )	pH	Water temperature (°C)	Turbidity (NTU)	Depth (m)
<i>Undisturbed</i>									
Mean	0.37	0.13	0.81	39.5	7.84	4.18	13.3	25.8	0.07
Median	0.09	0.07	0.56	28.9	8.82	4.17	14.1	1.9	0.13
Min	0.01	< 0.01	0.05	10.7	0.31	3.80	4.4	0.5	0.02
Max	2.87	0.51	4.35	140.2	15.5	4.70	20.5	750	0.16
<i>Restored</i>									
Mean	0.39	0.10	0.66	34.4	8.07	4.07	11.6	2.6	0.15
Median	0.10	0.08	0.60	35.0	8.55	4.08	12.4	1.4	0.07
Min	0.02	< 0.01	0.23	13.4	0.40	3.70	5.3	0.3	0.04
Max	5.31	0.37	1.83	59.3	17.3	4.70	18.2	34	0.37
<i>GLMM results</i>									
Region	t = -1.52 P = 0.23	t = -3.42 P = 0.04	t = -1.32 P = 0.28	t = -1.48 P = 0.23	t = 0.42 P = 0.70	t = 2.99 P = 0.06	t = -0.52 P = 0.64	t = -1.24 P = 0.30	t = 0.65 P = 0.56
Region:Pool type	t = 1.39 P = 0.26	t = 0.68 P = 0.55	t = -0.68 P = 0.55	t = -0.73 P = 0.52	t = 1.50 P = 0.23	t = 0.60 P = 0.59	t = 0.26 P = 0.81	t = -0.57 P = 0.61	t = -1.40 P = 0.26
Region:Pool type:Sampling date	t = -1.27 P = 0.23	t = -0.90 P = 0.39	t = -0.46 P = 0.66	t = 0.50 P = 0.62	t = -1.61 P = 0.13	t = 1.06 P = 0.31	t = 0.33 P = 0.75	t = 1.05 P = 0.32	t = -0.06 P = 0.95

whether there were significant differences in pool macroinvertebrate-community composition between region, pool type and sampling dates.

Macroinvertebrate community structure was summarised for each sample using the following measures: (i)  $\log_{10}$  (total abundance + 1); (ii) taxonomic richness; (iii) 1/Simpson's diversity index (1/S); (iv) taxonomic dominance (D) estimated as  $D = N_{\max}/N$ , where  $N_{\max}$  is the number of individuals in the most abundant species and N is the total abundance. Additionally, relative abundances (%) were calculated for macroinvertebrate indicator groups that are most commonly found in peatland pools (Mazerolle et al., 2006; Hannigan et al., 2011; Beadle et al., 2015): Chironomidae, Hemiptera, Coleoptera and Odonata. Beta-diversity was estimated using the Bray-Curtis index calculated across the replicate pool samples for undisturbed and restored, separately, on each sampling date. Mixed-effects general linear models (GLMM) were used

in the lme4 package in R (Bates et al., 2015) to determine whether there were significant differences in macroinvertebrate community metrics and pool physicochemical variables as a function of region (North or South Pennines), pool type (natural or restored; nested within region) and sampling date (three seasons; nested within pool type), with study sites and sampling date included as random factors.

To assess the assembly processes of macroinvertebrate communities, Jaccard's coefficient of similarity (J) was calculated for peatland pool samples collected in Sept. 2011, which was the first sampling occasion for each pool. J values were compared against those derived from 1000 null model simulations (Chase, 2007) for national (UK) and regional (Pennine study sites) species pools. The species pool used to construct national null assemblages was composed of the 64 taxa identified from our blanket peatland samples, plus an additional 159



**Fig. 2.** (a) Site and physicochemical variables (region denoted as NP = North Pennines, SP = South Pennines) - only significant variables ( $P < 0.05$ ) are shown [dissolved organic carbon (DOC)  $R^2 = 0.20$ ,  $P = 0.001$ ; pH  $R^2 = 0.08$ ,  $P = 0.01$ ; Dissolved Oxygen (DO)  $R^2 = 0.06$ ,  $P = 0.034$ ; Al  $R^2 = 0.27$ ,  $P = 0.001$ ; Fe  $R^2 = 0.12$ ,  $P = 0.002$ ]; (b) sites categorised by region and pool type (A = Artificial, N = Natural); (c) as per panel b for Sept. 2011; (d) as per panel b for March 2012; (e) as per panel b for June 2012; (f) species biplot. Non-metric fit  $R^2$  was 0.94, linear fit  $R^2$  was 0.71, and stress was 0.18.

macroinvertebrate taxa that have been reported from open water ponds throughout the UK (Pond Action, 1991; Nicolet, 2001; Nicolet et al., 2004; Hill and Wood, 2014). The peatland taxon pool that this analysis focused on is a subset of the national taxon pool. The peatlands that were restored had no ponds previously due to land drainage activities, and the restoration aimed to create ecosystems that are as similar as possible to those of the undisturbed, intact peatlands. Therefore, our aim with this analysis was to assess whether the communities that assembled from the national taxon pool in the restored site pools were similar to those on intact peatlands, which have also assembled from the same national taxon pool. The national taxon pool was used because immigration into restored peatlands would not be restricted exclusively to taxa found only on our study peatlands. However, if the restoration was successful then successful establishment of immigrants will mirror the intact peatland taxon pool. For comparative purposes, we created regional null models using only the 64 taxa found within our Pennine sampling pools. As these assemblages were already expected to be 'filtered' deterministically from the national species pool due to the peatland location, we expected to see a greater importance of stochastic assembly processes in this analysis reflecting between-pool differences. A key reason for evaluating restoration success using models across both scales was to identify whether the assembly processes were similar between pool types, regardless of the scale used to underpin the null models.

Null models were controlled for the taxonomic richness of each sample by randomly permuting the presence-absence of taxa within samples, using the permatfull procedure in Vegan. If community assembly was dominated by stochastic processes of dispersal/priority effects then observed and expected values would show no significant difference (i.e. mean observed values similar to mean null predictions) (Chase, 2007). Null modelling approaches based on taxonomic identity (Chase, 2007) were preferred over those based on biological traits (Brown and Milner, 2012) because of the overwhelming dominance of Chironomidae, for which traits are defined poorly below subfamily level. To determine effect sizes, null model estimates were subtracted from observed J values then compared between pool types  $\times$  region using GLM.

### 3. Results

#### 3.1. Macroinvertebrate community composition

From 120 individual pool samples, 28,217 individual macroinvertebrates were identified across 64 taxa. Most taxa belonged to the Chironomidae (28 taxa; 24,464 inds.), Coleoptera (11 adult taxa, 4 larval taxa;

1497 inds.) and Hemiptera (11 taxa; 318 inds.). Trichoptera were found in low abundance but included *Limnephilus coenosus* which is common in small permanent peatland pools, as well as Polycentropodidae (*Polycentropus* sp., *Plectrocnemia conspersa* and *Holocentropus* spp.). Small but significant differences in macroinvertebrate community composition were found between pool types (PERMANOVA;  $R^2 = 0.09$ ;  $P = 0.001$ ), region ( $R^2 = 0.17$ ,  $P = 0.001$ ) and pool type $\times$ region ( $R^2 = 0.09$ ;  $P = 0.001$ ) despite pool environments showing no significant differences in physicochemistry between pool types, either when combined overall or when nested within sampling dates (Table 1).

Samples collected in Sept. 2011 were most dissimilar, plotting in the positive regions of NMDS axis 1 compared with samples collected in 2012 (Fig. 2). Axis 1 of the NMDS was associated with shifts in composition from *Corynoneura scutella*, *Limnephilus coenosus*, *Polypedilum nubifer*, *Polypedilum nuberculosum* and *Helophorus brevipalpis* (negative region) to communities with more *Derotanyptus*, Nemouridae, Corixidae, *Chironomus plumosus* and *Tanytarsus numerosus* (positive region). Negative regions of axis 2 were associated strongly with *Pyrrhosoma nymphula*, and small *Hydroporus*, Orthoclaudiinae, Dytiscidae and Limnephilidae that could not be identified to genus or lower. Positive regions of axis 2 were associated with higher abundance of *Hydroporus pubescens*, *Hydroporus obscurus*, *Apsectrotanyptus trifascipennis* and *Psectrocladius (Allopectrocladius) obivius* (Fig. 2). Several physicochemical variables fitted significantly to the NMDS using ordifit, with higher pH and dissolved oxygen concentration associated with the samples collected in 2012.

#### 3.2. Community diversity metrics

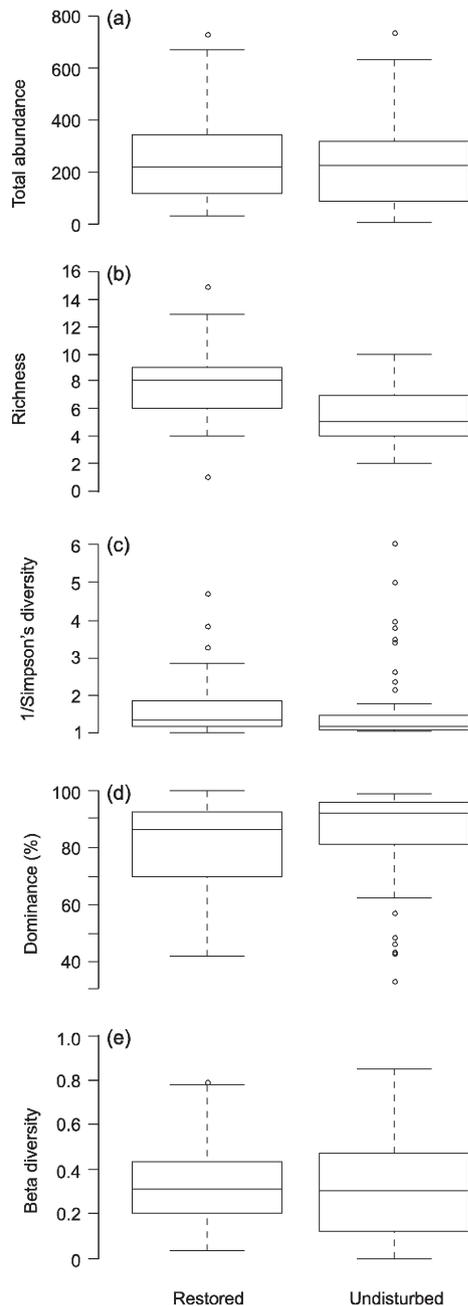
In contrast to the community composition findings, no differences were observed between region, pool type or sampling date for the macroinvertebrate metrics that we calculated (Table 2; Fig. 3). Chironomidae were typically the dominant indicator group and abundances were similar for both pool types at >80% on average (Fig. 4), numbering 100% in some pools (Table 2). No significant differences were found for Coleoptera, Hemiptera and Odonata relative abundance (Table 2, Fig. 4).

#### 3.3. Community assembly processes

Analysis of all pool samples combined revealed a mean beta-diversity (Jaccard's co-efficient of similarity [JJ]) of 0.34 (95% Confidence Intervals = 0.11–0.57) which contrasted markedly with predictions from 1000 null model assemblages (national scale mean J = 0.05; 95%

**Table 2**  
Descriptive statistics and GLMM results for undisturbed and restored peatland pool macroinvertebrate community metrics.

	Total abundance	Richness	Simpson's Diversity (1/S)	Dominance (D)	Beta diversity	% Chironomidae	% Hemiptera	% Coleoptera	% Odonata
<i>Undisturbed</i>									
Mean	226	5	1.6	84.5	0.31	82	1	11	0
Median	225	5	1.2	91.7	0.31	91.7	0	3	0
Min.	7	2	1.0	33.3	0	14	0	0	0
Max.	742	10	6.1	99.0	0.85	99	7	81	0
<i>Restored</i>									
Mean	244	8	1.6	80.4	0.33	80	2	9	0
Median	220	8	1.3	86.3	0.31	86.3	0	5	0
Min.	30	1	1	41.7	0.04	27	0	0	0
Max.	737	15	4.7	100.0	0.79	100	13	57	11
<i>GLMM results</i>									
Region	t = -0.41 P = 0.71	t = 1.90 P = 0.15	t = 0.88 P = 0.45	t = -1.07 P = 0.36	t = 1.83 P = 0.14	t = -0.84 P = 0.46	t = 1.00 P = 0.39	t = 0.39 P = 0.72	t = 1.13 P = 0.34
Region:Pool type	t = 0.88 P = 0.44	t = -0.86 P = 0.45	t = 0.67 P = 0.55	t = 0.13 P = 0.91	t = -1.13 P = 0.29	t = 0.21 P = 0.84	t = 0.72 P = 0.52	t = 0.22 P = 0.84	t = -0.59 P = 0.60
Region:Pool type:Sampling date	t = -1.97 P = 0.07	t = -0.65 P = 0.53	t = -0.51 P = 0.62	t = -0.32 P = 0.76	t = 0.42 P = 0.68	t = -1.13 P = 0.28	t = -1.39 P = 0.19	t = 1.42 P = 0.18	t = 0.00 P = 1.00



**Fig. 3.** Box plots of (a) Total abundance; (b) Richness; (c) 1/Simpson's Diversity; (d) Dominance and; (e) Beta diversity for pools on restored and undisturbed peatland.

CI = 0.04–0.06). For the national-scale null models, null model expectations were similarly low compared with within pool-type J (Undisturbed  $J = 0.39$  (95% CI = 0.17–0.61); null mean  $J = 0.04$ ; 95% CI = 0.03–0.05; Restored  $J = 0.42$  (95% CI = 0.20–0.64); null mean  $J = 0.06$ ; 95% CI = 0.05–0.07; Fig. 5a, b), with similar disparities between observed and null expectations evident when data were split by region. Effect-sizes between null expectations and observed values did differ slightly between regions (ANOVA  $F_{1,3997} = 1662$ ,  $P < 0.00001$ ) and pool type within regions (ANOVA  $F_{1,3997} = 2798$ ,  $P < 0.00001$ ).

For the regional-scale null models, within pool-type model expectations were also low (All data combined: mean  $J = 0.182$ ; 95% CI = 0.175–0.189; Undisturbed null mean  $J = 0.15$ ; 95% CI = 0.13–0.16; Restored null mean  $J = 0.22$ ; 95% CI = 0.21–0.24; Fig. 5c, d) compared with observed  $J$  values (as per national analysis above), but overlapped marginally with the lower 95% confidence intervals for the restored

pools indicating they were not significantly different. Effect-sizes between null expectations and observed values differed between regions (ANOVA  $F_{1,3997} = 21.182$ ,  $P < 0.001$ ) and pool type within regions (ANOVA  $F_{1,3997} = 51.739$ ,  $P < 0.001$ ).

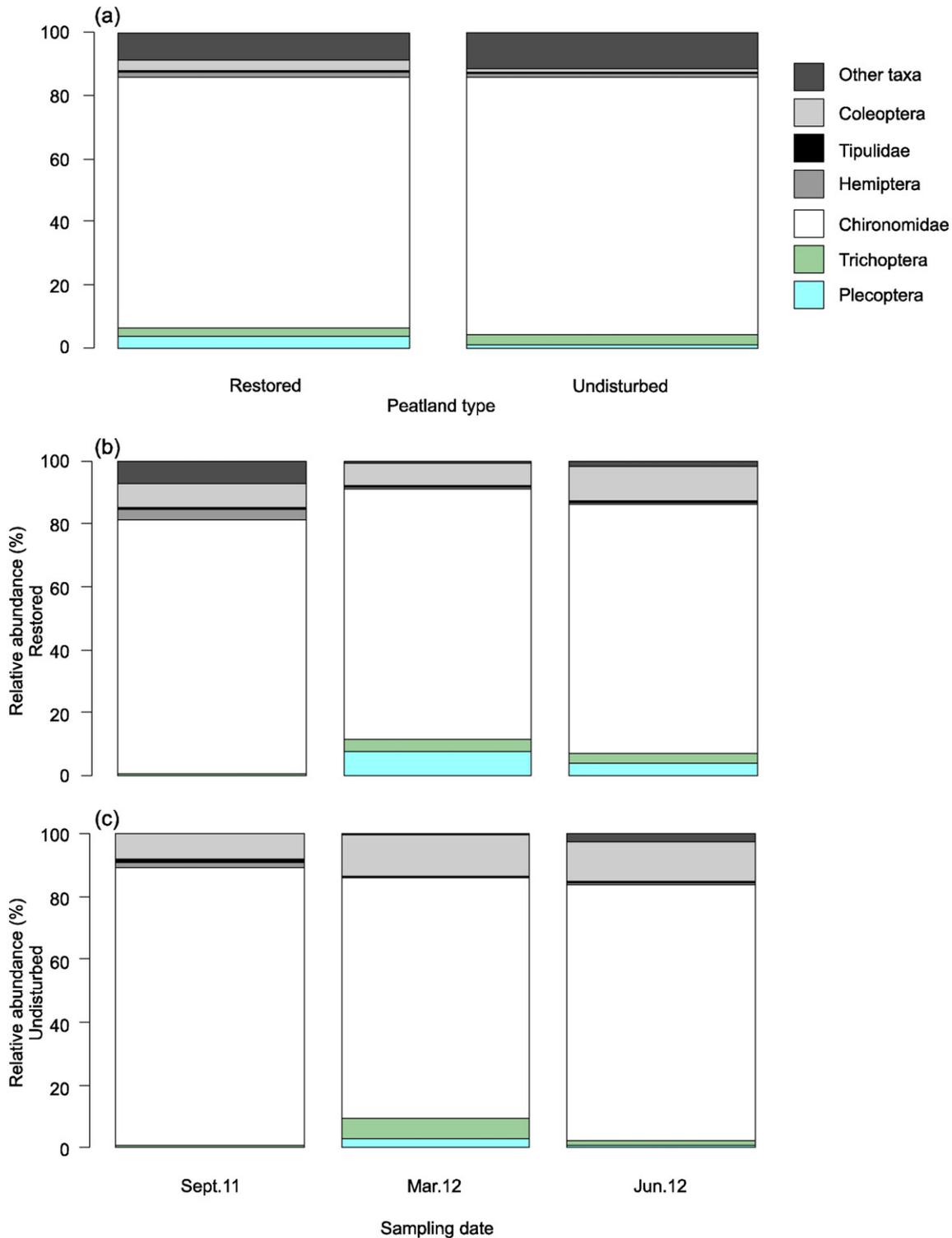
## 4. Discussion

### 4.1. Community composition and diversity

This study has provided detailed new insights into the biodiversity and community assembly processes of pool ecosystems on intact and restored blanket peatland. The dominance of Chironomidae in all pools was in agreement with findings from other bog pool studies (Beadle et al., 2015; Table 3). Three sub-families, Orthoclaadiinae, Chironominae and Tanypodinae, accounted for the majority of all the dipterans, similar to Hannigan et al's. (2011) study of peatland pools, and there was no significant difference in their abundance between pool types. The relatively low abundance of large invertebrate predators, the availability of refuge areas (e.g. among abundant moss layers) and/or mass-effects potentially contribute to the dominance of Chironomidae but experimental manipulations would be required to unpick these causes. Another reason for the dominance of Chironomidae may be their ability to adapt their diet to available food sources. All chironomid taxa, even tanypodids which are generally classed as predators, will consume detritus (Baker and McLachlan, 1979) which is abundant in peatland pools. Some chironomids also eat methanotrophic bacteria (Jones et al., 2008), and Ruse (2002) noted that many predatory chironomids are also algal-feeders during their early instars. This omnivory allows them to inhabit even the smallest of bog pools, such as puddles on Kielder Moor, northern England (Jackson and McLachlan, 1991).

Studies in mainland European and North American peatland pools have suggested that groups such as Coleoptera (Table 3) can sometimes dominate invertebrate communities, and they were typically the second most abundant group of macroinvertebrates found in our UK peatland pools. However, there were no significant differences in relative abundance between natural and artificial pools, most likely reflecting the similarity in pool physicochemical conditions. Adult Coleoptera have excellent flight capabilities (Mazerolle et al., 2006) and they readily colonise new peatland pool habitats (Table 3). Van Duinen et al. (2007) suggested that to evaluate the success of bog restoration for aquatic macroinvertebrates, it is important to examine the colonisation success of later colonisers such as caddis flies. In our study we observed *Limnephilus coenosus*, which is common in small permanent peatland pools (Wilkinson, 1984). Other caddis observed were Polycentropodidae (*Polycentropus* sp., *Plectrocnemia conspersa* and *Holocentropus* spp.). *Polycentropus* were found on only one occasion in an artificial pool at Middle Top Fell, and *Plectrocnemia* were found only in artificially formed pools at Winscar and Middle Top Fell. *Holocentropus* were found in both pool types but only in Sept. 2011. The presence of these caddis indicates that these pools are being colonised successfully by 'later colonisers' albeit in low abundance.

Odonata are represented widely in peat pools often being found in large permanent waterbodies (Standen, 1999; Mazerolle et al., 2006) perhaps reflecting the increased availability of prey or oviposition sites, as well as a need for permanent water coverage for the developing, often semivoltine, larvae. In this study, we found only one Odonata species, the damselfly *Pyrrhosoma nymphula*, at only one artificial pool site (Crook Burn), which is a low number of Odonata species compared to reports from restored peatlands in Finland where several species colonised pools within three years (Elo et al., 2015). All other studies of restored peatland have highlighted that new waterbodies are colonised by Odonata (Table 3), and as further studies of the many thousands of new UK peatland pool habitats are conducted, more records of Odonata should become available to better evaluate the provision of habitat for this group.

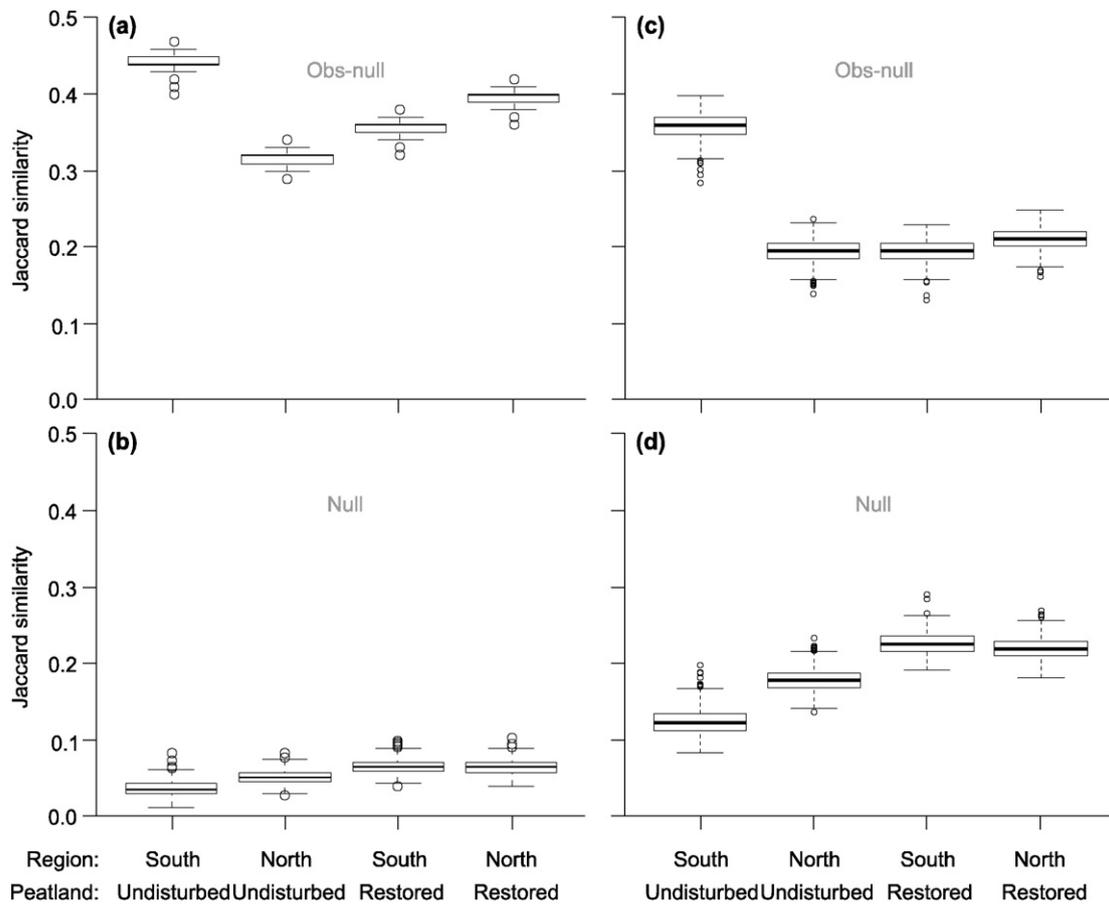


**Fig. 4.** Average relative abundance of selected macroinvertebrates groups from (a) all pool samples combined, and across the three sampling dates for (b) pools on restored peatland and (c) pools on undisturbed peatland.

#### 4.2. Community assembly

Our study provides a new perspective on the utility of incorporating null modelling approaches to evaluate the outcomes of ecosystem restoration, illustrating how conclusions about the success or otherwise in terms of biodiversity responses can be contingent upon the approach taken to evaluate ecological community properties. The two commonly used approaches of analysing community compositional differences

and/or comparing community diversity indices, produced conclusions about the effectiveness of peatland restoration that could initially be deemed as being in opposition. For example, when evaluating differences between undisturbed and restored peatlands using community diversity metrics, our findings of high similarity mirrored other peatland restoration studies (Hannigan et al., 2011) and suggested that the homogeneity of relatively harsh (i.e. low pH, low nutrient status (Hannigan et al., 2011; Turner et al., 2016)) pool environmental



**Fig. 5.** Pool type  $\times$  region boxplots for (a) Jaccard similarity scores for observed – null model predictions (regional null model); (b) null predictions only (regional null model); (c) Jaccard similarity scores for observed – null model predictions (local null model), and; (d) null predictions only (local null model).

conditions serves as a deterministic influence on community assembly (Verberk et al., 2010). In contrast though, significant (i.e.  $P < 0.05$ ) PERMANOVA results for pool type and region $\times$ pool type could be seen to imply that restored pools do not fully resemble the naturally formed pools in terms of their taxonomic composition, with restoration leading to different end points (Hobbs and Norton, 1996; Suding et al., 2004) despite the high similarity of pool environments. However, it is important to note that the effect size of pool type in these analyses was relatively small ( $R^2 = 0.09$ ); thus, the community composition of natural and restored pools was actually extremely similar for the most part. The minor differences could be attributable to random events of dispersal (Heino, 2012), and/or the establishment sequence of pool colonisers, for example via priority effects and biotic interactions with existing predators, prey and competitors (Belyea and Lancaster, 1999; Ledger et al., 2006).

Together, our findings from pool physicochemical habitat, biomonitoring metrics and community composition point towards these systems displaying an overwhelming deterministic nature, especially from the national species pool. The assembly models provided some evidence for a stochastic element within the regional species pool, although it was similar across the majority of pool locations and types, driving minor changes in community composition between pool types. Mixed assembly processes, such as those we have observed in these peatland pools, are increasingly recognised across a range of ecosystems (Thompson and Townsend, 2006; Brown and Milner, 2012; Vellend et al., 2014). However, to make robust conclusions about ecosystem restoration success requires an ability to determine more conclusively if these underlying fundamental processes vary or not *between* restored and reference conditions.

The marked contrast between national-scale null model expectations and observed community similarity values for pool macroinvertebrate communities, on both undisturbed and restored peatlands, confirmed the strong deterministic effect of peatland pool environment on community similarity (Chase, 2007). Effect-size estimates again suggested only minor differences in the strength of deterministic niche filters between the two regions and pool types compared with the overall magnitude of the observed vs. null effect-size. The regional null model analysis highlighted detectable differences in the importance of stochastic dispersal assembly processes although, notably, three of the four region/pool type combinations showed similar levels of stochasticity, offering further evidence of restoration success. Whilst the South Pennines restored pools were similar to those in the North Pennines, the South Pennines natural pools nevertheless showed more evidence of deterministic effects in the regional null model analysis compared with other locations. This might relate to a legacy effect from historic atmospheric pollution sources in this area (Evans and Jenkins, 2000) but more detailed chemistry data are needed to test this hypothesis. Overall, these analyses suggest that the incorporation of assembly process comparisons can potentially provide an additional useful benchmark for evaluating restoration success, than the measurement of community composition or biodiversity metrics alone.

Our novel approach to the evaluation of restoration schemes centres on the re-establishment of fundamental assembly processes relative to the reference state. Further work will clearly be needed to test this idea in other types of restored habitats. However, by adopting this concept more widely it should be possible to determine whether alternative end points of restoration (Suding et al., 2004) are a consequence of inadequate restoration approaches in which the assembly processes

**Table 3**  
A comparison of the key findings and conclusions from our study of UK blanket peatland aquatic ecosystems relative to published studies from other parts of Northern Europe and North America.

Key findings/conclusions from our UK study	Van Duinen et al. (2003) Netherlands(Van Duinen et al., 2003)	Verberk et al. (2006) Netherlands(Verberk et al., 2006)	Mazerolle et al. (2006) Canada(Mazerolle et al., 2006)	Verberk et al. (2010) Netherlands(Verberk et al., 2010)	Hannigan et al. (2011) Ireland(Hannigan et al., 2011)	Elo et al. (2015) Finland(Elo et al., 2015)*
Invertebrate taxonomic richness similar across pool types	✓				✓	
Invertebrate community structure of restored peatland pools similar to naturally-formed peat pools		✓		✓	✓	
Important habitats for diverse assemblages of Chironomidae	✓	✓		✓	✓	
Coleoptera colonised restored peatland pools readily	✓	✓	✓	✓	✓	
Odonata populations establish in restored peatland pools	✓	✓	✓	✓	✓	✓
Potential benefits for organisms other than invertebrates	✓ P		✓ Am, P			

Abbreviations: A – artificially-created pool on restored peatland; N – naturally-formed pool; P – plants; Am – amphibians; \* Elo et al. (2015) study focused only on Odonata.

themselves are not restored (i.e. true restoration failure), or whether unanticipated outcomes are an inherent feature of stochastic assembly processes creating different compositional end points (Lockwood and Pimm, 1999). In the latter, restoration might be classed as a failure owing to an ecological community composition not reaching a desired goal, yet this might actually be a Type II error (false negative) because restoration has recreated the inherent stochasticity of the reference system. In systems characterised by more stochastic assembly processes, restoration practitioners might need to acknowledge this fundamental process (Lockwood and Pimm, 1999; Chase, 2007) and accept 'success' once the ecosystem demonstrates an attainment of that state (i.e. observed community not significantly different from null expectations, similar to reference system), even if community composition and biodiversity metrics remain different from the reference state. In a strongly deterministic system such as the dystrophic peatland pools we focused on, there is a higher chance of restoration being deemed a success because community composition and biodiversity metrics are likely to converge on an end-point that is highly similar to the reference state. Restoration evaluations would therefore first need to determine the extent of deterministic versus stochastic processes in the planning stages, through the analysis of assembly processes in reference sites. This process-based information could be used subsequently to set realistic biodiversity goals for the restoration, and then evaluate post-restoration community assembly processes against this reference site community assembly benchmark.

## 5. Conclusions

Our results from UK peatland restoration schemes illustrate that there are strong similarities in terms of pool macroinvertebrate community composition to peatland pool assemblages across other parts of Europe and North America (Table 3), where rewetting has also created vast new expanses of open water (Verberk et al., 2010; Hannigan et al., 2011; Beadle et al., 2015; Elo et al., 2015). We have also demonstrated how large-scale peatland restoration can be deemed successful for standing freshwater aquatic biodiversity, adding to earlier studies showing benefits of these schemes for running water ecosystems (Ramchunder et al., 2012). These biodiversity gains might have the potential to act as a further impetus, alongside existing carbon sequestration targets, for businesses to invest in peatland restoration (IUCN Peatland Programme, 2015). While our study is the first to address the similarity of community assembly rules between restored peatlands and local reference conditions, the comparable community composition findings from a range of different northern peatlands suggest that the

similarity of assembly processes in both restored and undisturbed peatland pools could be generalizable. The characteristic low pH, low nutrient, waterlogged conditions of bog systems might also mean that restoration successfully recreates environments for re-establishment of ecological assembly processes in terrestrial ecosystem recovery.

Significant amounts of money in the order of billions of dollars have already been directed to peatland restoration (Ramchunder et al., 2012; Cris et al., 2014) and our approach to evaluating community assembly rules provides a new means of assessing the successful use of this funding for biodiversity gains. More generally, the overall costs of ecosystem restoration globally run into tens of billions of dollars each year (BenDor et al., 2015) but still a significant proportion of restoration schemes are deemed to be a failure (Benayas et al., 2009; Jones and Schmitz, 2009), often due to biodiversity goals not being met. Our demonstration of a new approach to evaluating restoration, that explicitly incorporates fundamental ecological theory, means that practitioners can begin to evaluate the influence of assembly processes on the biodiversity end-points reached after management interventions. Further development and incorporation of this approach into the planning, goal setting and evaluation stages of ecological restoration has the potential to lead to a step change in the number of ecological restorations deemed to be successful.

## Author contributions

Conceived of or designed study: LEB, JH, SJR.  
Performed research: SJR.  
Analysed data: LEB, SJR, JB.  
Wrote the paper: LEB, SJR, JB, JH.

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