Biodiversity and ecosystem functioning in natural bog pools and those created by rewetting schemes

Jeannie M Beadle, Lee E Brown and Joseph Holden

Anthropogenic drainage and cutting over of peatlands have historically occurred worldwide leading to erosion, issues with water quality, loss of biodiversity, and reduced rates of carbon accumulation. In recent years, rewetting measures have attempted to address these issues. Creating dams to block drainage ditches on peatlands is a common restoration tool, yet the ecological consequences of such management interventions are poorly understood. In particular, knowledge about the ecology of the thousands of pools created by drain blocking is limited even though they potentially provide valuable new habitat for aquatic species and food and water sources for terrestrial organisms. More research is needed to assess the suitability of these artificial pools as surrogates for naturally occurring peat pools with regard to the flora (e.g., bryophytes, algae, and macrophytes) and fauna (e.g., invertebrates and amphibians), which utilize them. Evidence suggests that (1) to maximize benefits to aquatic biota, land managers should consider creating an array of differently sized pools behind the dams as a broader size range would facilitate colonization by a wider range of taxa, (2) prioritizing landscapes close to existing water bodies would encourage faster colonization, and (3) even newly created pools with low macrophyte cover may be able to sustain substantial populations of larger fauna via algal primary production, consumption of detritus, and microbial processing of humic substances and methane. Ongoing programs of peatland restoration worldwide also afford unique opportunities to study how pool communities assemble and change over time. © 2015 The Authors. WIREs Water published by Wiley Periodicals, Inc.

How to cite this article:
WIREs Water 2015, 2:65–84. doi: 10.1002/wat2.1063

INTRODUCTION

Peat is an organic soil that consists of the slowly decaying remains of plant material (often Sphagnum spp.), which develops in waterlogged conditions.1 Peatlands that actively accumulate peat are referred to as mires2 and are important carbon sinks, which store approximately one third of the world’s soil carbon,3 although they have the potential to rapidly release it when they become degraded.4,5 Peatlands are subdivided into bogs, which are ombrotrophic (exclusively rain-fed), and fens, which are minerotrophic (influenced by groundwater). However, a peatland landscape may contain areas of both fen and bog. For example, while raised bog massifs (dome-like structures of peat) are indeed exclusively ombrotrophic,2 they can be found within a wider landscape which reflects a trophic gradient, including minerotrophic sources and transitional (lagg) zones.6 Likewise, blanket mires (in which peat cloaks the landscape in a layer that reflects the underlying topography) are mainly ombrotrophic (blanket bog) but may also contain areas of minerotrophic fen.2 Blanket mire is a globally scarce habitat, which

*Correspondence to: ill2jmb@leeds.ac.uk
water@leeds, School of Geography, University of Leeds, Leeds, UK
Conflict of interest: The authors have declared no conflicts of interest for this article.
The copyright line in this article was changed on 20 March 2015 after original online publication.
is especially well represented in the UK and Ireland. This review concentrates mainly on pools that form on areas of ombrotrophic bog, but takes into account trophic gradients when studies have looked at the wider peatland landscape, see Refs 6, 7.

Permanent pools are common features on many northern bogs (Figure 1). They constitute one of a series of nanotopes (small-scale structural elements also known as microforms) (Table 1) and there are many theories about how they form (cf. Ref 8). Pools situated entirely within a rain-fed peat profile are characterized by low pH, low levels of primary production and nutrients, but high levels of dissolved organic matter that stain the water brown, making the pools dystrophic rather than oligotrophic. However, pools that have any sort of minerotrophic input (e.g., those that are exposed to a mineral substrate) may differ from this pattern and have, for example, higher levels of pH. In general terms, ponds make a vital contribution to biodiversity, particularly at a landscape level, by sustaining a high richness (including rare) of macroinvertebrate species compared with other water bodies. In the 2007 UK species and habitat review, ponds were, therefore, added as a new priority habitat, along with dystrophic lakes. However, dystrophic bog pools that are known to house rare taxa including Red Data Book species and those with nationally notable status remain relatively understudied.

Degradation of blanket peat through drainage (an attempt to dry out and improve the land for forestry and farming) and cutting over (harvesting for peat-based products) has resulted in global problems including increased carbon emissions, loss of biodiversity and conservation issues (although see Chapman et al. for evidence that limited peat extraction may actually enhance biodiversity), and reduced water quality. However, peatlands have a high conservation value and are one of the habitats listed in the RAMSAR agreement, ‘Sphagnum acid bogs’ are listed under Annex 1 of the EU habitats directive and blanket bog is also a UK Biological Diversity Action Plan priority habitat. In recent years, emphasis has been placed on rewetting peatlands to try and restore them to a fully functional, revegetated state, and the benefits of rewetting for carbon sequestration have been recognized on an international scale by the Kyoto protocol. By far the most common restoration method adopted in blanket peatlands around the world is to dam drainage ditches creating pools of water behind each dam (Figure 2). The dams (and therefore the pools) are typically spaced evenly along the length of the drain and, being constrained by the drain dimensions, are similar in size, unlike pools in natural systems, which can vary substantially in area and depth.

In the British Isles, many thousands of these artificial pools have been created to restore peatland hydrology. In many areas (e.g., much of the Pennines), pools in blocked drains form the only pool complexes within the peatland, thus extending the aquatic landscape to new frontiers and providing habitat for aquatic species as well as vital food and water sources for the many species of moorland birds that utilize blanket bog. However, the ecological status of these artificially created pools is almost unknown with only two reports looking at their macroinvertebrate assemblages in the British Isles. In the Netherlands, van Duinen et al. studied pools on areas of raised bog created by rewetting measures and in Canada, Mazerolle et al. studied pools that they had dug themselves on an area of restored peatland. Other studies have looked at the aquatic ecology of restored peatlands but concentrated on water bodies that already existed prior to restoration. For example, Verberk et al. sampled bog pools, ditches, and puddles of different water types (e.g., minerotrophic/ombrotrophic) both before and after rewetting measures on a heterogeneous bog remnant in the Netherlands.
TABLE 1 | Classification of Nanotopes (Surface Features) Found on Ombrotrophic Bogs in Britain (Reprinted with permission from Ref 2. Copyright 2010 R A Lindsay)

| Terrestrial (T) Microforms | Code | Name       | Description                                                                 |
|----------------------------|------|------------|------------------------------------------------------------------------------|
| T1                         | Low ridge | Occupies a vertical range of $\sim 0$ to 15 cm above the average water table. Generally the most species-rich zone. |
| T2                         | High ridge | Occupies the vertical zone of $\sim 15$ to 25 cm above the average water table. Forms the predominant nanotope for blanket bog where there is a distinct slope, and for bogs that have suffered some degree of human impact. |
| T3                         | Hummock | Occupies the vertical zone of $\sim 25$ to 1 m above the average water table. Invariably formed by moss growth. |

| Aquatic (A) Zones | Code | Name                     | Description                                                                 |
|------------------|------|--------------------------|-----------------------------------------------------------------------------|
| A1               | Sphagnum hollow | Occupies the vertical zone of $\sim 0$–10 cm below the average water table. Dominated by a more-or-less continuous carpet of the aquatic Sphagnum cuspidatum. |
| A2               | Mud bottom hollow | Shallow pools no more than 20 cm deep. Has no dense, continuous mat of Sphagnum, merely scattered pockets of either S. subsecundum or S. cuspidatum. |
| A3               | Drought-sensitive pool | Occupies the vertical zone of $\sim 20$–40 cm below the average water table. Has an evident expanse of open water, though there may also be loose floating mats of Sphagnum cuspidatum or S. subsecundum. |
| A4               | Permanent pool   | Pools that may be 3–4 m deep, extending almost to the mineral subbase, with solid, vertical walls. Consists largely of an open water body in which some detritus and a range of aquatic invertebrates can be found. |

The aim of this review is to provide guidance for land managers involved in drain-blocking schemes on areas of bog who wish to maximize ecological benefits to the aquatic communities in the newly created pools. We provide some contextual background to the formation of natural pools and the creation of those formed by rewetting measures, before reviewing the literature on the ecology (macroinvertebrates, amphibians, and primary producers) of both pool types. We then focus on macroinvertebrates and assess the main factors driving the community composition in bog pools to help underpin predictions about community assembly in drain-blocked pools on areas of ombrotrophic bog. Based on the evidence outlined in the following sections, Figure 3 provides a conceptual model of the potential ecological development of drain-blocked bog pools through time, with corresponding suggestions for research questions.

NATURAL POOLS

Formation, Distribution and Morphology
Open water bog pools have been reported from every continent except Antarctica and form one of a series of nanotopes that contribute to the patterning characteristic of bogs (Table 1). Under the right conditions, pool complexes can be extensive. For example, small, open water features ($<1$ km$^2$) cover up to 77% of the surface area of minerotrophic peatlands in high boreal Quebec, Canada. In the British Isles, the presence of permanent open water pools is generally restricted to the most northerly, oceanic areas, making them especially prevalent in areas of Scotland where, in strongly patterned areas such as parts of the Flow Country, pools may cover up to half of the surface area.

The formation and development of bog pools is strongly related to the local hydrological regime and its interaction with the prevailing climate and topography (e.g. Ref 33). These factors also interact with vegetation to determine the form and extent of the patterning (e.g. Ref 36). Many authors provide evidence for the role of differential rates of peat accumulation and the processes surrounding decay (e.g. Ref 8). Recently, advances in technology such as Ground Penetrating Radar (GPR) have enabled the potential links between the positioning of some pools and the underlying geological features (e.g., esker crests formed by glacial retreat) to be identified.

Volume 2, March/April 2015 © 2015 The Authors. WIREs Water published by Wiley Periodicals, Inc.
Morphologically, the dimensions of natural pools on blanket bog are generally constrained by the depth of the peat profile; therefore, they are typically shallow with a large surface-area-to-depth ratio. Fundamentally, this structure affects the ecology of the pools; vegetation is able to colonize further into the center of the water body, although high levels of turbidity can constrain this process leading to mainly open water pools. Shallow pools also do not exhibit the seasonal thermal stratification seen in larger lakes and they are more susceptible to reduced water levels in periods of drought.

**Primary Producers**

Although some natural bog pools are heavily vegetated, the macrophyte diversity is low. In the British Isles, bog pool vegetation is limited to a few aquatic *Sphagnum* species such as *S. cuspidatum* and *S. auriculatum*, sundews such as *Drosera intermedia*, the sedges *Carex rostrata* and *Eriophorum angustifolium*, and the bog bean *Menyanthes trifoliata*. This pattern seems to be repeated globally. For example, a study of natural bog pools in Canada found a similar community structure, dominated by *Sphagnum* mosses, other mosses, and liverworts, with lower coverage of ericaceous shrubs, e.g. *Chamaedaphne calyculata* (leather leaf) and *Vaccinium oxyccoccos* (bog cranberry), Carex grasses and sundews (e.g. *Drosera rotundifolia*). While *Sphagnum* is seen as the major vegetation component in bog pools, algal communities are also present. Microalgae disperse between water bodies via animal vectors (e.g. birds, water beetles), but there is also some evidence for airborne dispersal via the wind, especially for green algae (see Ref 40). Although *Sphagnum* generally contributes much more than algae to primary production in wetland habitats, there is evidence that algae form an important constituent of the food webs in bog pools. A study by van Duinen et al. undertaken in a pristine raised bog in Estonia found algae to be an important basal component in the diets of consumers. Isotopic analysis suggested that periphyton (of which green algae was the major component) sustained approximately half of the invertebrate population, but results also implied that different species of algae might be responsible for sustaining the entire invertebrate food web.

A study of the phytoplankton communities of pools on raised bog in Tierro Del Fuego, Argentina, found distinct assemblages in different pools, which appeared to be driven mainly by physical variables (pool area and mean depth), with shallower pools displaying higher levels of algal density and species richness. Nováková found that algal communities in subalpine peat pools in the Czech Republic were dominated by diatoms and desmids, with shallow, peaty pools displaying the highest levels of biodiversity. In the British Isles, recent scientific literature on bog pool algae is notably scarce, since Lund described several new and rare Chrysophyceae (golden algae) found in peat pools in the Lake District. However, a recent in-depth and systematic study of desmid communities found along the hummock-lawn-pool nanotope gradient in Scottish blanket mire systems has greatly enhanced our understanding of British peat pool algal communities, and also provided evidence for a new species of desmid, of the genus *Staurastrum*.

**Macroinvertebrates**

Table 2 lists papers that have reported on the macroinvertebrate communities in naturally occurring water bodies on areas of bog along with the taxa identified. In the British Isles, much of the literature on macroinvertebrate communities living in blanket bog water bodies is based in the Flow Country of Caithness and Sutherland, Scotland, where study sites are readily available (Table 2). This body of work is...
supplemented by studies from Ireland and England, although studies based in England are rare due to the relative paucity of naturally occurring pools. The size of the water bodies studied ranges from temporary puddles to larger lakes and meres (shallow lakes) (Table 2). The taxa identified most often in these studies are Coleoptera (beetles), Diptera (true flies), Ephemeroptera (mayflies), Hemiptera (true bugs), Odonata (dragonflies and damselflies), and Trichoptera (caddisflies). Other taxa include Araneae (spiders); small crustaceans such as amphipods, copepods, and cladocerans (water fleas); Hirudinea (leeches); Hydracarina (water mites); Hymenoptera (e.g., wasps, bees); Megaloptera (e.g., alderflies); Oligochaeta(worms); Orthoptera (e.g., crickets); and Tricladiida (flatworms). Stoneflies (Plecoptera) were listed in only one study where the species Nemoura cinerea was present in the Korenbargerven nature reserve in the Netherlands. The scarcity of stoneflies in peat pool studies can perhaps be explained by the fact that they are cold water stenotherms, rarely found in water above 25 °C, and are adapted to live almost exclusively in oxygenated, running waters. Their presence in the still waters of bog pools is an interesting development and perhaps suggests the importance of such habitats as refuge for species not usually associated with them. Gastropods were absent from these studies, which is probably explained by the acidic water containing insufficient calcium ions for shell building.

With regard to rare and vulnerable species, in the Flow Country, northern Scotland (blanket bog), Towers recorded three beetle species with Nationally Notable status: Dytiscus lapponicus, Illybius aenescens, and Gyrinus minute along with the IUCN British Red Data Book caddisfly species Nemotaulius punctatolineatus. A baseline survey of acid-mire invertebrates in Dartmoor, England, made prior to restoration, found two water beetle species Paracymus scutellaris and Helochares punctatus classified as nationally Scarce Category B by Foster. Verberk et al. found the rare chironomid, Lasiodiamesa gracilis, in oligotrophic pools in their study site in the Netherlands. However, and perhaps unsurprisingly, peatlands with a trophic gradient have been shown to house more rare and endangered aquatic species than do purely ombrotrophic bogs. Studies from the Netherlands, looking at

---

**FIGURE 3** Conceptual framework showing how the different ecological elements of drain-blocked pools on areas of ombrotrophic bog might develop and interact over time from the moment of pool creation (i.e., since blocking), along with associated research questions.

- **Fauna**
  - New pools - bacteria already present in the peat
  - Early colonisers active fliers (e.g. beetles)
  - Arrival of weak fliers & passive dispersers (e.g. via phoresy)
- **Carbon sources**
  - Production driven by MOB / bacteria consuming DOC
  - Rates of photosynthesis increase along with algal PP
  - Macrophyte / sphagnum PP further boosts photosynthesis
- **Flora**
  - New pools lack vegetation cover - mainly open water
  - Pioneer algal species arrive via animal and wind vectors
- **Physical and chemical**
  - Low nutrient levels and low pH (unless substrate exposed)
  - pH decreases as sphagnum cover increases
  - Community assembly influenced by pool size / permanence

---

**Suggested research questions**

- How does the macroinvertebrate species composition change over time?
- Do macroinvertebrate communities in drain-blocked pools resemble those of natural pools?
- Is there increased usage by birds and amphibians over time?
- Are the pools net heterotrophic or autotrophic?
- What are the relative contributions of PP, MOB and DOC as basal sources of carbon?
- Does the contribution of PP increase with plant / moss cover and does this influence trophic status?
- How does the algal species composition change over time?
- Does increased habitat heterogeneity contribute to greater faunal diversity?
- Is there a change in macroinvertebrate functional feeding groups with increased vegetation cover (e.g. fewer carnivores, more herbivores?)
- Can pool size thresholds be defined which relate to different assemblages of macroinvertebrates?
- Does pool size influence pool selection by amphibians or birds?
- Are pool dimensions or water chemistry more important in defining community assembly?
## TABLE 2 | A Selection of Peatland Pool Macroinvertebrate Studies by Location Along With Taxa Identified

| Study Site | Water Body | Ara | Col | Cru | Dip | Eph | Hem | Hir | Hyd | Hym | Meg | Odo | Oli | Ort | Ple | Trich | Tricl |
|------------|------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|-------|
| **Caithness and Sutherland, Scotland** | | | | | | | | | | | | | | | | | |
| Foster45* | Loch Fleet Bog pools | ✓ | ✓ | | | | | | | | | | | | | | |
| Downie et al.46 | Badanloch bog Bog pools | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | | | | | |
| Standen et al.52 and Standen58 | Loch nan Clar & Woodcock Hill Bog pools | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | | | | | |
| Towers12 | Forsinard Bog pools | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | |
| **England and Ireland** | | | | | | | | | | | | | | | | | |
| Jackson and McLachlan49* | Kielder Moor, Northumberland (Eng) Temporary puddles | | | | | ✓ | ✓ | | | | | | | | | |
| Crisp and Heal50* | Connamara (Ire) Moor House (Eng) Lakes, tarns, pools, & reservoirs | | | | ✓ | ✓ | | | | | | | | | | |
| Gibbons51 | Blake Mere, Staffordshire (Eng) Mere | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | |
| Boyce52* | Dartmoor (Eng) Bog pools | ✓ | | ✓ | ✓ | | | | | | | | | | | | |
| Hannigan et al.53 | Kippure/Liffey Head Bog (Ire) Bog pools | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | | | | | |
| Drinan et al.13* | West of Ireland Lakes & meres | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | | | | | |
| **Canada, Estonia & The Netherlands** | | | | | | | | | | | | | | | | | |
| Verberk et al.25, Verberk et al.54, Verberk et al.57 | Korenburgerveen (Netherlands) Various-raised bog landscapes | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | | | |
| Van Kleeft et al.56* | Estonia & the Netherlands Various-raised bog landscape | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | | | | | |
| Mazerolle et al.32 | New Brunswick (Canada) Bog pools | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | | | | | | |

Papers marked with * studied only the taxa indicated in the table.

Ara, Araneae; Col, Coleoptera; Cru, Crustacea; Dip, Diptera; Eph, Ephemeroptera; Hem, Hemiptera; Hir, Hirudinea; Hyd, Hydracarina; Hym, Hymenoptera; Meg, Megaloptera; Odo, Odonata; Oli, Oligochaeta; Ort, Orthoptera; Ple, Plecoptera; Trich, Trichoptera; Tricl, Tricladida.

Pools situated throughout a raised bog remnant with water chemistry ranging from oligotrophic to minerotrophic, reported many rare beetles including *Colymbetes paykullii* and the seriously threatened species *Haliplus fulvicollis*, which was found in pools influenced by seepage water. A study undertaken in a pristine raised bog in Estonia found six species of vulnerable, endangered, or critically endangered Trichoptera, of which five were far more prevalent in transitional or lagg zones than in the ombrotrophic bog massif. However, the literature suggests that bog pools may be especially important for rare or endangered odonates, such as three of Scotland’s rarest species, *Aeshna caerulea* (the Azure Hawker), *Somatochlora arctica* (the Northern Emerald), and *Leucorrhinia dubia* (the White-Faced Darter). Six species of critically endangered, endangered, or vulnerable odonates were found in intact raised bog in Estonia, including *Coenagrion hastulatum* (the Northern damselfly), of which three were more prevalent in the bog massif (ombrotrophic) and three in the transitional or lagg zones. Towers recorded the presence of *C. hastulatum* in Scotland and Drinan et al. found the endangered species *Cordulia aenea* (the Downy Emerald) in Ireland.

### Amphibians

Results from a Canadian study looking at artificial and natural bog pools identified four amphibian taxa associated with the pools; green frogs (*Rana clamitans melanota*), leopard frogs (*Rana pipiens*), wood frogs (*Rana sylvatica*), and the American toad (*Anaxyrus americanus*). Tadpoles as well as metamorphosed juveniles and adults were also present. Amphibian occurrence was much higher in artificial than natural bog pools, although there was no relationship detected between amphibian abundance and pool size, pool depth, or pH. The only strong relationship
found was a negative one between the occurrence of green frog tadpoles and the cover of herbs and floating vegetation. In contrast, a study by Hunter et al., in the Kosciuszko National Park, New South Wales, Australia, found that the males of the critically endangered Southern Corroboree Frog (*Pseudophryne corroboree*) selected nest sites in the banks of larger and deeper pools, with a weaker positive relationship between occupied male nest sites and midday pool temperature. A study of amphibians living in a range of fens in a reserve near Nijmegen, the Netherlands, found six anuran species including the common frog (*Rana temporaria*) and the common toad (*Bufo bufo*). The results indicated that spawning did not take place in the most acidic water (pH 3.7), most likely due to the increased occurrence of the spawn being attacked by the freshwater mould *Saprolegnia*. The presence of mould decreased as pH increased and was virtually nonexistent in water with a pH of approximately 6. In the British Isles, although amphibians such as the common toad (a UK BAP priority species), the smooth (*Lissotriton vulgaris*) and palmate (*Lissotriton helveticus*) newts, and the common frog are known to utilize pools on blanket bogs, the quantitative literature is rare. One example is Dibner et al., who analyzed how the common frog utilized pools in mature plantation forests, clear-felled areas, unplanted blanket bogs, and roadside drainage ditches in the West of Ireland. The results indicated a clear preference for roadside drainage ditches as breeding sites. Other studies looking at, for example, the pool occupancy rates or the relative importance of amphibians as top-level predators in the absence of fish, are needed to build on these interesting findings.

### POOLS CREATED BY RESTORATION MEASURES

**Background**

Globally, peatlands have been subjected to anthropogenic drainage for a variety of reasons. For example, in southeast Asia, vast swathes of tropical peatlands have been drained to facilitate agriculture and forestry, leading to increased CO₂ emissions. Harvesting peat for fuel or horticultural products is also a widespread practice and occurs in areas with some of the world’s largest peat deposits such as Russia and Canada. In the UK, drainage of upland blanket peat was actively encouraged by the Government after World War II and subsidized at 70% of the cost. The closely spaced drains across blanket peat landscapes were originally cut with the intention of drying out peat to develop upland terrain for agriculture, mainly improving sheep grazing and red grouse habitat, and for afforestation. (Figure 4). Drainage reached a peak in the 1960s and 1970s, especially in the English Pennines, with aerial photographs of England and Wales suggesting that in some areas, more than 50% of blanket bog and moorland had been drained and in Scotland, some 5000 km² of uplands had been subjected to drain development.

The British upland drainage policy is now widely regarded as having been unsuccessful, with no evidence that the original aims were met, e.g. Ref. 23. Furthermore, there is evidence that drainage was detrimental. In addition to the erosion caused by the drainage itself, further degradation was triggered by the increased stocking rates of large grazing animals. Side effects of degraded peatlands included decreased carbon accumulation rates and increased dissolved organic carbon (DOC) loads and water discoloration in peatland streams. Ecologically, drainage altered biodiversity by lowering the water table, resulting in a loss of vegetation adapted to the waterlogged conditions and negative impacts on downstream river biodiversity. Thus, a process of drain blocking was started in the UK in the late 1980s with the main aim of encouraging water table recovery and thus the establishment of peat-forming species, notably *Sphagnum* mosses.

The potential consequences of drain blocking have been the subject of research which has concentrated mainly on hydrological aspects with a legal and more direct financial implication, such as levels of DOC and water discoloration that require treatment for potable supply. In contrast, the ecological implications have received scant attention, despite the stated aim of many schemes to restore pre-drainage ecological conditions. One study based in Northern...
England looked at the impact on stream macroinvertebrates and physicochemistry, another analyzed the impact of drain blocking on cranefly larvae in the peat adjacent to blocked drains, and a third looked at vegetation colonization in pools formed by drain blocking. With regard to macroinvertebrates, some studies have looked at the impact of peatland restoration on existing lentic water bodies. However, there are only two reports dealing with the macroinvertebrate communities which inhabit drain-blocked pools in peat systems in the British Isles (but see van Duinen et al. for a study based on a restored raised bog in the Netherlands).

The need to analyse and quantify the potential ecological benefits of drain blocking is urgent, as there is some evidence to suggest that open water pools on areas of peatland may act as hot spots for emissions of greenhouse gases, especially methane. Another potential issue is that pools may increase the abundance of the dipteran family Ceratopogonidae (biting midges), which are known to spread diseases, such as the Schmallenberg virus, among sheep. These potentially detrimental impacts of drain blocking need to be balanced with the possible ecological benefits as the new pools may provide valuable habitat for algae and invertebrates and also food and water for amphibian and bird species. Therefore, any decision on possible drain-blocking methodologies needs to be informed by a solid evidence base.

**Primary Producers**

Studies on vegetation in drain-blocked pools are scarce. Mazerolle et al. undertook a study on a previously mined and partially restored peatland near Quebec City (Canada) in which eight artificial pools were created and the vegetation growth monitored and compared to the nearby natural pools. After 4 years, the artificial pools still exhibited substantially less vegetation cover than the natural pools. In particular, mean *Sphagnum* cover was only 21.6% compared to 89.5% in the natural pools. In contrast, Peacock et al. studied 60 drain-blocked pools on a blanket bog in north Wales and found that pools revegetated quickly, displaying a mean total vegetation cover of 76% just 18 months after restoration. This apparent discrepancy may be explained by the varying levels of CO₂ in the water, as low levels have been shown to limit the growth of the aquatic *Sphagnum* species *S. cuspidatum*. Levels of CO₂ may vary due to the abundance of methanotrophic bacteria living alongside the moss, which oxidize methane to produce CO₂ but CO₂ data were not available for the two studies. Shallower pools in the North Wales study were dominated by *Eriophorum* sedges whereas deeper pools exhibited more *Sphagnum* coverage, and two pools exhibited substantial algal growth. In newly created pools with limited vegetation cover, algal growth can be substantial and may contribute significantly to the food web.

There is evidence that drain-blocked pools promote algal biodiversity, as artificial pools at Moor House NNR (English Pennines) were recently reported to house *Saturnella saturnus*, a species previously unreported in the British Isles (Figure 5). A study by Goodyer (2014) looked at how desmid communities reacted to both drainage and drain blocking in Scottish blanket mires. Results showed that desmid species richness was very low in drained peatland, compared to a nearby intact mire, but that it did recover, after drain blocking, to approximately 70% of the diversity of the nearby intact peatland after 12 years.

**Macroinvertebrates**

A study by van Duinen et al. of various raised bogs in the Netherlands compared macroinvertebrate communities found in remnant pools (formed in old peat cuttings or buckwheat trenches abandoned 50+ years ago) and restored pools (created by rewetting measures no longer than 29 years previously). The pools housed five provisional red-list beetles species as...
defined by Drost et al.\textsuperscript{77} and the red-listed odonates \textit{Leuchorrhina dubia} (the White-Faced Darter) and \textit{Coenagrion lunatum} (the Crescent Bluet or Irish Damselfly), along with four red-listed caddisflies. In Canada, Mazerolle et al.\textsuperscript{32} found only Coleoptera, Hemiptera, and Anisoptera in eight pools they had dug on an area of restored peatland before 4 years. The species found were not reported as being rare or endangered, but the authors did note that the beetle species included several peatland specialists such as \textit{Colymbetes paykulli} and \textit{Hydrobius fuscipes}.

In southern England, the Exmoor Mire Restoration project, undertaken by South West Water, carried out a survey of invertebrates (terrestrial and aquatic) on areas of blanket peatland subjected to drain blocking.\textsuperscript{30} Four aquatic taxa were targeted by pond netting; Odonata, Hemiptera, Coleoptera, and Diptera (Tipuloidea – craneflies). Although no Red Data Book species were identified, the authors listed several key species including the acid-mire specialists \textit{Sympetrum danae} (Black Darter dragonfly) and the water boatman species \textit{Hespercorixa castanea}. Among the beetle species was the acid-mire obligate \textit{Helochares punctatus}, which is classified as Nationally Scarce Category B.\textsuperscript{59} Ramchunder et al.\textsuperscript{27} provided initial findings from a study looking at 20 natural and 20 drain-blocked pools in the English Pennines. Twenty six macroinvertebrate species had been identified to date encompassing Hemiptera, Coleoptera, Trichoptera, Plecoptera, Diptera (crane-flies and chironomids), and Odonata (damselflies). These findings generally agree with the existing British Isles–based literature on natural pools, especially with regard to the dominance of chironomids, beetles, and true bugs. The presence of stoneflies (Plecoptera) in this study was especially interesting as this taxon was listed in only one other study reviewed for this paper,\textsuperscript{7} when the occurrence of one species, \textit{Nemoura cinerea}, was found to have increased following rewetting measures in a raised bog remnant in the Netherlands. However, the British-based study reported only preliminary findings and did not provide the species of stoneflies found, but did report that stoneflies were captured in both types of pools (natural and artificial).

Amphibians
A study looking at amphibians in artificial pools, based in Canada, involved pools dug on peatland by the authors.\textsuperscript{32} The results showed that use of artificial pools by amphibians was substantially higher than use of naturally occurring pools; for example, the mean number of green frog tadpoles found in 70 natural bog pools was 2.1 ± 10.8, whereas it was 22.9 ± 64.8 in just eight man-made pools. These findings indicate that drain-blocked pools may provide a vital addition to the habitat range of these taxa, although the sampling took place in different years (1999–2000 for the natural pools and 2003 for the artificial pools), so differences due to other factors (e.g., weather) cannot be ruled out. However, a study by Dibner et al. in the West of Ireland also found that artificial water bodies (in this case roadside drainage ditches) were utilized more by the common frog than other natural water bodies in the same area.\textsuperscript{62} One potential reason for this may be that drainage ditches provide useful connectivity within the landscape. If this is the case, then drain-blocked pools in drainage systems on areas of bog may well prove to be similarly useful.

ENVIRONMENTAL INFLUENCES ON MACROINVERTEBRATE COMMUNITY COMPOSITION

The factors that enable ponds to contribute so much to landscape-scale diversity; their isolated nature, small catchment areas, and heterogeneous physicochemical attributes,\textsuperscript{9,78} also lead to low levels of inter-pool community similarity. This, along with the often stochastic nature of community assembly,\textsuperscript{79} can make it difficult to compare pools and analyze the potential mechanisms driving the processes of colonization and the subsequent community assembly. However, some factors known to play a part in the community structure of lentic habitats are discussed here, with a view to explain the pool macroinvertebrate communities described above. These factors will be considered to identify which could be the most influential in shaping community assembly in pools created by rewetting measures on areas of bog. However, it must be noted that pool characteristics often combine to shape community structure, so there is some inevitable overlap between the sections.

Pool Size/Permanence
Ecologists have long observed a positive relationship between habitat area and the number of species found there, a phenomenon referred to as the ‘species-area’ curve.\textsuperscript{80} One explanation for this is that larger areas usually encompass more habitat types.\textsuperscript{81} However, MacArthur and Wilson\textsuperscript{82} expanded upon this with the equilibrium theory of island biogeography, which argued that both the size and the isolation of an island play a part in the number of species present by helping to determine the balance between immigration and extinction. Lentic water bodies are effectively habitat islands, with smaller pools especially prone to
stochastic extinction events such as extreme temperature fluctuations and desiccation. In this way, pool size and permanence are inextricably linked and together play a vital role in shaping their aquatic communities. However, it has also been posited that small, isolated water bodies may be an exception to the theory of island biogeography, at least for certain taxa. These authors argue that the impact of species interactions, namely, the absence of top predators (i.e., fish) from such habitats, means that the relative abundance and species richness of other taxa (e.g., macrophytes, macroinvertebrates, and amphibians) can flourish. The absence of fish also promotes a more species-rich and complex pool vegetation structure. Thus, small, fishless water bodies will house more macroinvertebrate taxa per unit area than larger lakes containing fish. However, although bog pools are fishless, they are known to be home to amphibians and are frequented by moorland birds that may act as top-level predators.

Oertli et al. analyzed data from 80 ponds across Switzerland, including bog pools, which were assigned to different size classes. While increased size correlated with increased richness and abundance, the relationships were fairly weak for most taxa with the exception of Odonata and Gastropoda. Odonates are widely represented in peat pool studies where they have been found to dominate in larger, more permanent pools. This could be due to several factors such as increased availability of prey or oviposition sites, but may also be because their relatively longer, often semivoltine, life cycle requires the protection of permanent water coverage for the developing larvae, as is the case with *Aeshna juncea* (Common Hawker) (Figure 6). However, another of the species commonly found in bog pool studies – *Sympetrum danae* (Black Darter) – has a univoltine life cycle, so may be equally able to thrive in smaller pools.

For other species, the relationship is less clear. Towers studied 22 natural bog pools in a complex in Forsinard, Scotland, and found only a weak, nonsignificant relationship between pool size and species richness. The author theorized that this may be because all the pools across the size gradient had similar vegetation structures and also were in close proximity to each other, allowing cross colonization of an already impoverished species pool. Drain-blocked pools will also meet these criteria, being similar in structure and closely grouped together. The analysis of Towers did, however, show a change in community composition along a patch-size gradient, with at least one size-related character (perimeter, area, or depth) always proving important in explaining community composition. For example, depth was the only significant variable explaining Dytiscid beetle assemblages in baited traps, probably as they actively use the water column for predation. Similarly, in a study by Mazerolle et al. in Canada, the capture rates of Hemipterans in natural peat pools were positively correlated with pool perimeter, potentially because many Hemipterans (e.g., Gerridae) make use of the pool surface.

Several studies have found that small pools tend to house small beetles. Standen et al. showed that temporary pools (Table 1) in the Flow Country of Scotland were dominated by small beetles of the subfamily Hydroporinae. In another study in the Flow Country, Downie et al. found no individuals from the anatomically largest subfamily (Dytiscinae) in the smallest pools in their study, which instead were dominated by the comparatively smaller Hydroporinae and Colymbetinae. A study by Foster of peat pools at Loch Fleet, Scotland, also found that shallow pools were dominated by small diving beetles (genus *Hydroporus*) whereas deep pools housed the comparatively larger diving beetles (genera *Agabus* and *Ilybius*). These findings may be suggestive of a level of niche differentiation, with smaller and larger beetles potentially dividing resources to avoid direct competition. All dytiscids are predators, both as larvae and adults, so will compete for the same food sources, but smaller species should be able to fulfil their nutritional requirements in a smaller water column. However, all beetles with a univoltine life cycle—that includes a summer larvae and overwintering adult phase (e.g., the larger *Agabus arcticus*)—will be able to take advantage of smaller, temporary pools in the summer for larval development.

Pools of different sizes may promote biodiversity due to their exploitation by species with different functional traits and life histories. Verberk et al.
analyzed macroinvertebrate datasets from a range of water bodies located in the Korenburghervaart nature reserve (the Netherlands), including bog pools. They found that, while large and small bog pools were relatively similar with regard to the life-history strategies of the macroinvertebrates inhabiting them, small, shaded bog puddles differed slightly as species needed to be able to react to more unstable water levels. Species addressed this in different ways, with resistant diapausing stages or with relatively long-lived adults capable of dispersal during dry periods. This indicates that even very small pools can be useful to a range of macroinvertebrates.

The above studies suggest that, while there is a relationship between increased pool size and changes in community composition, it is a complex one underpinned by other variables, both biotic and abiotic.

The size of pools formed in drains will be constrained by the drain dimensions and the topography of the terrain. If, however, one of the objectives of blocking on a particular site is to encourage colonization by a wide range of aquatic macroinvertebrates, then land managers could consider creating a range of differently size pools by manipulating the shape of the drains directly behind the dam, both vertically and horizontally. It seems reasonable to assume, for example, that the creation of larger pools may especially benefit taxa with semivoltine life cycles (i.e., life cycles that take more than one year to complete) by affording more stability and protection for the developing larvae. Such taxa include some species of dragonflies and damselflies, which are among the most charismatic taxa to inhabit pools on blanket bog.

Habitat Heterogeneity

The link between higher levels of habitat heterogeneity and increased biodiversity is a well-established ecological theory. The theory assumes that more complex habitats (usually referring to the range of vegetation structure present) provide more niches for species to exploit and, therefore, promote increased biodiversity. Previously, habitat heterogeneity has been regarded simply as part of the species–area curve theory (see section 4.1); but increased size does not always lead to increased structural heterogeneity, and bog pools are a good example of this. For example, in British peat pools macrophytes are generally limited to a few species, mainly aquatic Sphagnum species and Eriophorum sedges, and this relative homogeneity of vegetation was one theory posited by Towers to explain the lack of a species–area relationship in her work looking at bog pools of different sizes at Forsinard. In this section, we look at the influence on macroinvertebrate communities of (1) the structural complexity within an individual pool and (2) the diversity of habitats within the wider landscape.

Different taxa of aquatic beetles are known to make use of different mesohabitats such as pool surfaces (e.g., Gyrinidae), water column (e.g., Dytiscidae), and steep-sided pool edges (e.g., larger species of Dytiscidae), while others utilize Sphagnum carpets and vegetation mats. Indeed, variance in the morphology of different beetle species (e.g., body shape, size, leg configuration) dictates their swimming capability, particularly the balance between velocity and maneuverability and, therefore, whether the species is more suited to open water (i.e., pool center) or more densely vegetated habitats (i.e., pool margin). This was reflected in a study by Verberk et al. in the Netherlands, which found a clear link between invertebrate locomotion and microhabitat preference. However, Downie et al. found no significant difference in either individual abundance or in community composition between pool center and edge for Coleoptera or Hemiptera in a study based in the Flow Country. In contrast, a study of peatland restoration measures in Canada by Mazerolle et al. found that capture rates of some macroinvertebrate taxa were influenced by different types of pool vegetation. Capture rates of beetles and damselflies were negatively associated with the presence of tall shrubs and emergent vegetation, whereas those of Hemiptera were negatively associated with the occurrence of low shrubs and moss cover. Capture rates of damselflies increased among submerged and floating vegetation. Thus, encouraging the colonization of different types of vegetation may increase macroinvertebrate diversity in drain-blocked pools, although the practicality of this process is untested. For example, Mazerolle et al. found that an attempt to encourage vegetation colonization by stocking half of their artificial pools with aquatic vegetation, including Sphagnum cuspidatum, from nearby sources had no significant impact on subsequent vegetation growth compared to the unstocked pools.

Landscape heterogeneity, as opposed to within-pool heterogeneity, may also be a factor in determining the levels of biodiversity. Verberk et al. looked at how restoration (rewetting) measures impacted on macroinvertebrate communities in areas of raised bog with water bodies along a trophic gradient (and, therefore, increased landscape heterogeneity) in the Netherlands. The authors found that rewetting led to an overall decrease in biodiversity, with common species increasing in numbers and rarer, characteristic species declining. However, the study areas in this report were on raised bog with pockets of...
minerotrophic input among the ombrotrophic areas, meaning that there was more inherent heterogeneity (and, therefore, probably more macroinvertebrate diversity) than would be found on blanket bog, which tends to have a more constant nutrient status. Thus, the homogenizing potential of rewetting measures would be, by definition, greater on areas of heterogeneous raised bog than on its blanket counterpart. Also, many of the areas in England subjected to drain blocking do not have naturally occurring pools prior to restoration, so there are far fewer existing aquatic populations that can be adversely impacted by the measures.

**Pool Age**

Ecological succession, defined as ‘the sequential replacement of species following a disturbance (a relatively abrupt loss of biomass or structure),’ is a well-established ecological theory. The communities of most habitats change through time due to many reasons, e.g., species–environment interactions, species–species interactions, and stochastic or neutral factors such as birth, death, colonization, extinction, and speciation. Community assembly is dictated by three main factors as discussed by Belyea and Lancaster: dispersal constraints, environmental constraints, and internal dynamics, and it is reasonable to assume that macroinvertebrate communities in newly created pools will differ from those in long-established pools as a result of these factors. For example, pool age was found to be the most important factor determining beetle assemblage in 18 freshwater lowland ponds in Pennsylvania, USA, with predatory dytiscids prevailing in young ponds and herbivorous species in older ponds with more developed vegetation communities. However, a study in a heterogeneous bog remnant in the Netherlands found that deterministic processes and stochastic processes operated simultaneously, but that their relative importance varied for species with different life-history traits; habitat generalists were more influenced by stochastic processes (e.g., colonization and extinction rates) and habitat specialists by deterministic processes (e.g., environmental conditions).

The age of many natural peat pools is unknown, but drain-blocking measures provide an ideal opportunity to analyse community assembly in lentic habitats by monitoring floral and faunal succession in pools from the moment of pool creation. Also, as land managers usually keep detailed records about when drains are blocked and as pools form almost immediately behind the dams, pools can be reliably aged and chronosequence (space for time) studies may be undertaken.

There is some evidence that older pools house more rare and characteristic bog species than younger pools. A study by van Duinen et al. on areas of remnant and restored raised bog in the Netherlands, found that the older remnant water bodies (at least 50 years old) housed more fairly rare, rare, and very rare species than the younger restored pools (no more than 29 years old), as well as more species classified as characteristic of raised bog systems. In a shorter-term study in Canada, Mazerolle et al. dug eight pools in an area of peatland formerly subjected to peat extraction but now undergoing restoration measures. After 4 years, invertebrate abundance and species richness were still substantially lower in the man-made pools as opposed to those in the natural pools in nearby, relatively undisturbed peatlands. However, in a study on restored blanket bog in County Wicklow, Ireland, Hannigan et al. found no significant difference in macroinvertebrate communities between natural pools on an intact peatland and those on a bog restored before 15 years. Taken together as a timeline, these three studies suggest that artificial pools may come to more resemble the more established/natural pools with increased age, although this is likely to happen over a period of decades rather than years (so chronosequence studies may be more time effective than those based on direct observation). Thus, it seems probable that the communities in drain-blocked pools could develop over time to provide suitable long-term habitats for aquatic species if they were allowed to persist. Of course, this also depends on the suitability of the pools themselves (environmental factors) and the availability of nearby ‘source’ communities. Another point to note is that larger, deeper pools would be more likely to remain as open water systems; so if the establishment of aquatic macroinvertebrate communities is a consideration in peatland restoration measures, then the creation of at least some larger pools should be considered.

**Dispersal of Aquatic Invertebrates**

Aquatic invertebrates are usually classified as either passive or active dispersers (Figure 7). Active dispersal is achieved by adults with flying capabilities, whereas passive dispersal is accomplished via animal vectors or transport by wind. A further type, temporal dispersal, could be defined as the ability to survive through periods of unsuitable environmental conditions (e.g., dormant propagules stored in sediment or diapause) (Figure 7). Neighboring pools are more likely to exhibit similar community composition
than those farther apart due to two main factors: (1) ponds closer together are likely to have similar environmental conditions that suit certain taxa and (2) invertebrate dispersal occurs in fragmented populations between reachable, suitable habitats, leading to the existence of meta-populations.

In England, although drain-blocked pools in the same drainage system are very close to each other, initially they do not often have a ‘source’ macroinvertebrate community close by, due to the lack of naturally occurring pools. Instead, colonizing invertebrates potentially come from tarns or sink holes, or valley bottom lakes and streams, but these are often sparse and isolated. It seems likely, therefore, that initial colonization of drain-blocked pools may be slow but that once a few pools in a system are invaded, then the capacity to spread out along the entire drainage system would increase. Also, the more drainage systems are blocked, the more pools are created and cross colonization between areas is facilitated. This is reflected in a study of lowland urban ponds, which found a highly significant correlation between macroinvertebrate species richness and pond density (i.e., more species were found in ponds that were close together). Furthermore, a study by Verberk et al. found that adjacent water bodies in a heterogeneous bog remnant were more similar than environmental conditions would have anticipated. This suggests that invertebrates will disperse to nearby water bodies even if environmental conditions are not ideal, so prioritizing areas of drained bog close to existing water bodies for blocking will facilitate the dispersal of invertebrates across the wider landscape.

Predatory dytiscids (Coleoptera) have been shown to be early colonizers of newly created pools. A likely explanation for this is that flight is an important element of the life cycle of the vast majority of adult water beetles. For example, the strong flight capacity of Colymbetes paykulli, a beetle restricted almost entirely to the cold water of sphagnum bogs, was demonstrated by Mazerolle et al. This species colonized a man-made pool in Canada within 2 years of its creation when the nearest natural pools were 40 km away. As with beetles, some adult hemipterans are able to actively disperse via flight and, therefore, may also be among the first to colonize drain-blocked pools. Evidence for this was provided by Mazerolle et al. who dug eight pools in an area of Canadian peatland. After 4 years, Hemiptera and Coleoptera accounted for almost the entire invertebrate community in the man-made pools, suggesting that they are effective early colonizers.

Passive dispersal is a risky strategy, as an organism has no control over its final destination. Hence, many passive dispersers have evolved adaptations to increase their chances of success. These include physical features such as hooks and sticky appendages to facilitate adhesion to an animal vector, and also phenological adaptations, which include timing the production of the bulk of small dispersing stages to coincide with bird migrations. In the case of drain-blocked pools, passive dispersal via bird vectors could prove to be a successful mechanism as moorland birds are attracted to areas of blanket bog with many pools and, due to the drainage systems in which they form, drain-blocked pools often occur in large numbers and in close proximity to each other.

**Water Chemistry and Gases**

One element of water chemistry which has been shown to be important in dictating community composition in at least some lentic habitats, is pH. However, studies concentrating specifically on peat bog pools have generally discounted pH as a contributory factor when explaining community composition. This is likely due to the fact that pH levels in peat bog pools are kept consistently low, typically < pH 4.5 in areas dominated by Sphagnum. Readings from studies in the Flow Country, Scotland, vary very little, for example, from just below 3.5 to just above 4.5 and such restricted ranges are unlikely to account for much variation in species assemblages. In a more heterogeneous raised bog landscape, the pH range is greater and does contribute to higher levels of biodiversity (e.g., Ref 6).

Bog pool studies that measure pH levels do not always measure other chemical properties such as electrical conductivity (EC), nutrient levels, or dissolved oxygen. Towers measured EC and total dissolved solids (TDS) but did not relate either to community composition. Nutrient levels in peat pool water are generally low, with Hannigan et al. reporting that that levels of nitrite, nitrate, and ammonia were too low to be detected (<0.001 mg l⁻¹), and with pools also exhibiting low conductivity, ranging from 50.5 to 55.67 μS cm⁻¹. It seems that such properties are seen as unimportant in defining bog pool communities, perhaps because readings are consistently so low and / or unvaried. However, in this respect as with pH, drain-blocked pools may differ from natural (ombrotrophic) pools if they have eroded down to the underlying mineral substrate.

**Food Webs and Carbon Cycling**

The low levels of primary production in bog pools have traditionally been attributed to the low levels of nutrient availability, although a recent study
by Karlsson et al.\textsuperscript{106} proposed that light availability (affected by colored organic matter input) could be the main limiting factor in unproductive lakes. In bog pools, such allochthonous (external) sources of organic carbon are readily available because of the high levels of dissolved organic carbon (DOC) in the surrounding peat, a large part of which is made up of humic substances.\textsuperscript{68} These substances drain into the pools providing a source of organic carbon for bacteria, which is independent of the within-pool primary production and may mean that peat pools are net heterotrophic (i.e., they respire more carbon than is fixed via photosynthesis). Many studies looking at the ratios of Gross Primary Production (GPP) and Ecosystem Respiration (ER) in a range of lentic systems, using the dissolved oxygen change technique,\textsuperscript{107} have reported negative Net Ecosystem Production (NEP) values, suggesting they are net heterotrophic and thus biological sources of carbon to the atmosphere.\textsuperscript{108–110} If this proves to be the case with artificial peat pools then, from a climate change perspective, this would constitute a negative aspect, which land managers would need to consider alongside the potential benefits to biodiversity afforded by pool creation.

Using isotopic analysis, van Duinen et al.\textsuperscript{42} set out to establish the relative contribution of different basal food sources in bog pools in Estonia. The results indicated that zooplankton relied mainly on bacteria, and insects on algae, with periphyton (dominated by green algae) estimated to sustain approximately half of the invertebrate food web (Figure 8). Methane-oxidizing bacteria (MOB) were believed to contribute to the food web both directly (i.e., consumed by zooplankton and chironomid larvae) and indirectly, by releasing CO$_2$, which was then assimilated by the algae in the pools and passed up the trophic levels (Figure 8). The potential importance of methane as a basis for food webs in lentic habitats was also suggested by a study of Australian billabongs, in which carbon isotope analysis found that macroinvertebrates were too$^{13}$C-depleted to have derived their carbon purely from pool vegetation.\textsuperscript{111} The authors hypothesized that methanotrophic bacteria may have been an important source of carbon despite the large biomass of littoral and fringing biomass in the pools. It then seems likely that the presence of humic substances and methanotrophic bacteria may help to sustain substantial macroinvertebrate communities in drain-blocked pools before, and even after, large-scale vegetation colonization.

**CONCLUSION**

Natural peat pools house important communities of macroinvertebrates, including many acidi-mire specialists and rare and endangered species. Creating new artificial pools on peatlands may have conservation benefits by extending the habitat range for such species. However, a distinction should be made between water bodies on areas of blanket bog, such as those studied in the British Isles, e.g., Refs 12, 52, 53 and the heterogeneous raised bog remnants studied in the Netherlands, e.g.,\textsuperscript{25} with the latter having more inherent biodiversity due to the different water and
vegetation types studied. Whereas large-scale rewetting has proved to be somewhat detrimental to diversity in the Netherlands, this may not be the case on areas of blanket bog such as those in the British Isles, where the rewetting measures are unlikely to impact on existing water bodies and instead will generally create new freshwater habitat. The creation of drain-blocked pools in areas without natural pool systems is also likely to attract moorland birds and amphibians, thereby benefitting the wider ecosystem.

In areas of blanket peat, pool size and water-level stability appear to be major factors in defining species assemblages, with smaller, astatic pools home to different communities than larger, permanent pools. Therefore, land managers looking to create pool systems for the benefit of macroinvertebrates should consider creating an array of pools of different sizes by manipulating the physical dimensions of the drains immediately behind the dams. Guidelines on the actual size ranges for drain-blocked pool systems that would help to promote aquatic biodiversity could be deduced from empirical studies. More studies on amphibians are also needed to determine the main physico-chemical variables underpinning their pool selection behavior, so that this can be taken into account during drain-blocking planning. Amphibians may also be important as top-level predators in these fishless pools, although this theory is also as yet untested.

The literature on naturally occurring lentic water bodies suggests that drain-blocked pools should be net heterotrophic, and that both algae and allochthonous sources of organic carbon should form an important basal element of the food webs in these systems. Further studies to ascertain the rates of GPP, ER, and NEP would help to elucidate the issue, as would the analysis of the carbon isotopes found in the various food sources and consumers. If the pools prove to be biological carbon sources, then this would need to be considered alongside the potential ecological benefits to biodiversity. Whether more heterogeneous vegetation cover promotes macroinvertebrate diversity is unclear from the literature. However, as the morphology and life-history traits of different species make them suited to either open water or more densely vegetated areas, it seems likely that a heterogeneous vegetation structure that includes open water areas would be beneficial. However, the practicality of inducing Sphagnum to grow in pools poses problems and the process of seeding pools with Sphagnum is still in its infancy.

The literature suggests that macroinvertebrates will attempt to colonize nearby water bodies even when environmental conditions are not ideal.
Therefore, land managers should consider prioritizing catchments for drain blocking which are near to existing water bodies, such as streams, tarns, and sinkholes, and then working outwards. This will maximize the chances of successful dispersal by the existing biotic communities. Monitoring could begin as soon as the pools form, to look at initial community assembly and ascertain how long it takes for different taxa to colonize the pools. If long-term monitoring is not an option, then pools belonging to different age classes could be sampled to analyse how the communities change over time. The literature from the Netherlands looking at raised bog pools suggests that older pools tend to house more diverse communities, including more species classified as rare or characteristic. It remains unknown if this is the case in blanket bog pools.

Drain-blocked pools could prove to be an important addition to the ecological landscape of blanket mires, not just for aquatic species but for terrestrial biota as well. Baseline datasets on the taxa that inhabit them are vital not just for current understanding but also to enable monitoring in the face of climate change and the increased likelihood of extreme weather events such as drought. The large number of pools created by these measures should act as a buffer against such disturbances and may eventually provide refuge for taxa from more marginal habitats, which respond to the changing climate by migrating upward and poleward. Peatland rewetting measures constitute a rare case of freshwater habitat creation and their biodiversity should, therefore, be carefully managed and monitored to maximize the potentially large-scale ecological benefits.

**ACKNOWLEDGMENT**

The research was supported by a NERC CASE studentship in partnership with the RSPB.

**REFERENCES**

1. Bragg OM, Tallis JH. The sensitivity of peat-covered upland landscapes. *CATENA* 2001, 42:345–360.

2. Lindsay RA. Peatlands and carbon: a critical synthesis to inform policy development in peatland conservation and restoration in the context of climate change. Report to RSPB Scotland, Scottish Natural Heritage, Natural England, Forestry Commission, Countryside Council for Wales, IUCN UK Peatlands, 2010.

3. Yu Z, Loisel J, Brosseau DP, Beilman DW, Hunt SJ. Global peatland dynamics since the Last Glacial Maximum. *Geophys Res Lett* 2010, 37:L13402.

4. Holden J. Peatland hydrology and carbon release: why small-scale process matters. *Philos Trans R Soc A Math Phys Eng Sci* 2005, 363:2891–2913.

5. Baird A, Holden J, Chapman P. Defra Project SP0574. A literature review of evidence on emissions of methane in peatlands, 2009.

6. van Duinen GA. Rehabilitation of aquatic invertebrate communities in raised bog landscapes, 2013.

7. Verberk WCEP, Leuven RSEW, van Duinen GA, Esselink H. Loss of environmental heterogeneity and aquatic macroinvertebrate diversity following large-scale restoration management. *Basic Appl Ecol* 2010, 11:440–449.

8. Belyea LR, Lancaster J. Inferring landscape dynamics of bog pools from scaling relationships and spatial patterns. *J Ecol* 2002, 90:223–234.

9. Williams P, Whitfield M, Biggs J, Bray S, Fox G, Nicolet P, Sear DA. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biol Conserv* 2003, 115:329–341.

10. JNCC. Report on the Species and Habitat Review. Report by the Biodiversity Reporting and Information Group (BRIG) to the UK Standing Committee, June 2007.

11. Maitland PS. New horizons—new species? The invertebrate fauna of unexplored aquatic habitats in Scotland. *Aquat Conserv Mar Freshw Ecosyst* 1999, 9:529–534.

12. Towers NM. Invertebrate community structure along a habitat-patch size gradient within a bog pool complex, 2004. Vol. PhD.

13. Drinan TJ, Foster GN, Nelson BH, O’Halloran J, Harrison SSC. Macroinvertebrate assemblages of peatland lakes: assessment of conservation value with respect to anthropogenic land-cover change. *Biol Conserv* 2013, 158:175–187.

14. Silvola J, Alm J, Ahlholm U, Nykanen H, Martikainen PJ. CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *J Ecol* 1996, 84:219–228.

15. Hooijer A, Page S, Canadell JG, Silvius M, Kwadijk J, Wosten H, Jauhiainen J. Current and future CO₂...
emissions from drained peatlands in Southeast Asia. *Biogeosciences* 2010, 7:1505–1514.

16. Littlewood N, Anderson P, Artz R, Bragg O, Lunt P, Marrs R. Peatland Biodiversity, 2010. Available at: http://www.iucn-uk-peatlandprogramme.org/publications/commission-inquiry/work-commission/peatland-biodiversity. (Accessed August 21, 2014).

17. Carroll MJ, Dennis P, Pearce-Higgins JW, Thomas CD. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. *Glob Chang Biol* 2011, 17:2991–3001.

18. Chapman S, Buttler A, Francez A-J, Laggoun-Défarge F, Vasander H, Schloter M, Combe J, Grosvernier P, Harms H, Epron D, et al. Exploitation of northern peatlands and biodiversity maintenance: a conflict between economy and ecology. *Front Ecol Environ* 2003, 1:525–532.

19. Holden J, Chapman PJ, Labadz JC. Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. *Prog Phys Geogr* 2004, 28:95–123.

20. Armstrong A, Holden J, Kay P, Francis B, Foulger M, Gledhill S, McDonald AT, Walker A. The impact of peatland drain-blocking on dissolved organic carbon loss and discolouration of water: results from a national survey. *J Hydrol* 2010, 381:112–120.

21. UN. Convention on Wetlands of International Importance especially as Waterfowl Habitat. Ramsar (Iran). UN Treaty Series No. 14583. As amended by the Paris Protocol, 3 December 1982, and Regina Amendments, 28 May 1987, 1971.

22. EU. Council of European Communities Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, 1992, 7–49.

23. Holden J, Shotbolt L, Bonn A, Burt TP, Chapman PJ, Dougill AJ, Fraser EDG, Hubacek K, Irvine B, Kirkby MJ, et al. Environmental change in moorland landscapes. *Earth Sci Rev* 2007, 82:75–100.

24. Joosten H, Tapio-Biström M-L, Susanna T. Peatlands – guidance for climate change mitigation through conservation, rehabilitation and sustainable use. *Mitigation of Climate Change in Agriculture (MIICCA) Programme*, 2012, Vol. 5.

25. Verberk WCEP, Kuper JT, van Duinen GA, Esselink H. Changes in macroinvertebrate richness and diversity following large scale rewetting measures in a heterogeneous bog landscape. *Proc Neth Entomol Soc Meet* 2006, 17:27–36.

26. Armstrong A, Holden J, Kay P, Foulger M, Gledhill S, McDonald AT, Walker A. Drain-blocking techniques on blanket peat: a framework for best practice. *J Environ Manage* 2009, 90:3512–3519.

27. Ramchunder SJ, Brown LE, Holden J. Biodiversity of natural and artificial upland blanket peat bog pools: preliminary scientific findings, May 2012.

28. Downie IS, Coulson JC, O’Connell MJ, Whitfield DP. Invertebrates of importance to breeding birds in the flow country. In: Standen V, Tallis JH, Meade R, eds. *Patterned Mires and Mire Pools: Origin and Development: Flora and Fauna: Proceedings, University of Durham, 6–7 April 1998*. London: British Ecological Society; 1998.

29. Buchanan GM, Grant MC, Sanderson RA, Pearce-Higgins JW. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis* 2006, 148:615–628.

30. Boyce DC. Invertebrate survey of Exmoor MIRE blanket bog sites, 2009. Report to Exmoor National Park Authority, 2010.

31. van Duinen G-JA, Brock AMT, Kuper JT, Leuven RSEW, Peeters TMJ, Roelofs JGM, van der Velde G, Verberk WCEP, Esselink H. Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. *Wetl Ecol Manage* 2003, 11:447–459.

32. Mazerolle MJ, Poulin M, Lavoie C, Rochefort L, Desrochers A, Drolet B. Animal and vegetation patterns in natural and man-made bog pools: implications for restoration. *Freshw Biol* 2006, 51:333–350.

33. Glaser PH. The distribution and origin of mire pools. In: Standen V, Tallis JH, Meade R, eds. *Patterned Mires and Mire Pools: Origin and Development: Flora and Fauna: Proceedings, University of Durham, 6–7 April 1998*. London: British Ecological Society; 1998.

34. Connolly J, Talbot J, Pelletier L. Mapping peatland pools to improve estimations of carbon store on a boreal peatland in Canada. *Geophys Res Abstr* 2014, 16 EGU2014–5526.

35. Lindsay RA. *Bogs: The Ecology, Classification and Conservation of Ombrotrophic Mires*. Scottish Natural Heritage: Perth; 1995.

36. Eppinga M, Rietkerk M, Wassen M, De Ruiter P. Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. *Plant Ecol* 2009, 200:53–68.

37. Comas X, Slater L, Reeve AS. Pool patterning in a northern peatland: Geophysical evidence for the role of postglacial landforms. *J Hydrol* 2011, 399:173–184.

38. Mataloni G, Tell G. Comparative analysis of the phytoplankton communities of a peat bog from Tierra del Fuego (Argentina). *Hydrobiologia* 1996, 325:101–112.

39. Nováková S. Algal flora of subalpine peat bog pools in the Krkonose Mts. *Preslia* 2002, 74:45–56.

40. Kristiansen J. Dispersal of freshwater algae – a review. *Hydrobiologia* 1996, 336:151–157.

41. Sigee DC. *Freshwater Microbiology: Biodiversity and Dynamic Interactions of Microorganisms in the Aquatic Environment*. Chichester: John Wiley & Sons; 2005.
42. van Duinen GA, Vermonden K, Bodelier PLE, Hendriks AJ, Leuven RSEW, Middelburg JJ, van der Velde G, Verberk WCEP. Methane as a carbon source for the food web in raised bog pools. *Freshw Sci* 2013, 32:1260–1272.

43. Lund JWG. New or rare british chrysophyceae. I. *New Phytol* 1949, 48:453–460.

44. Goodyer E. Quantifying the desmid diversity of scots blanket mires. Vol. PhD, University of Aberdeen, 2014.

45. Foster GN. Evidence for pH insensitivity in some insects inhabiting peat pools in the loch fleet catchment. *Chem Ecol* 1995, 9:207–215.

46. Downie IS, Coulson JC, Foster GN, Whitfield DP. Distribution of aquatic macroinvertebrates within peatland pool complexes in the Flow Country, Scotland. *Hydrobiologia* 1998, 377:95–105.

47. Standen V, Rees D, Thomas CJ, Foster GN. The macro-invertebrate fauna of pools in open and forested patterned mires in the Sutherland flows, North Scotland. In: Standen V, Tallis JH, Meade R, eds. *Patterned Mires and Mire Pools: Origin and Development: Flora and Fauna: Proceedings, University of Durham, 6–7 April 1998*. London: British Ecological Society; 1998.

48. Standen V. Quantifying macroinvertebrate taxon richness and abundance in open and forested pool complexes in the Sutherland Flows. *Aquat Conserv Mar Freshw Ecosyst* 1999, 9:209–217.

49. Jackson JM, McLachlan AJ. Rain-pools on peat moorland as island habitats for midge larvae. *Hydrobiologia* 1991, 209:59–65.

50. Crisp DT, Heal OW. Diversity and distribution of aquatic meso- and micro-fauna in mires. In: Standen V, Tallis JH, Meade R, eds. *Patterned Mires and Mire Pools: Origin and Development: Flora and Fauna: Proceedings, University of Durham, 6–7 April 1998*. London: British Ecological Society; 1998.

51. Gibbons DS. From observation to experiment. In: Standen V, Tallis JH, Meade R, eds. *Patterned Mires and Mire Pools: Origin and Development: Flora and Fauna: Proceedings, University of Durham, 6–7 April 1998*. London: British Ecological Society; 1998.

52. Boyce DC. Invertebrate survey of blanket bog on Dartmoor, 2010. Report to Dartmoor National Park Authority, 2011.

53. Hannigan E, Mangan R, Kelly-Quinn M. Evaluation of the success of mountain blanket bog pool restoration in terms of aquatic macroinvertebrates. *Biol Environ Proc R Irish Acad* 2011, 111B. 95–105.

54. Verberk WCEP, van Duinen GA, Brock AMT, Leuven RSEW, Siepel H, Verdonschot PFM, van der Velde G, Esselink H. Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. *J Nat Conserv* 2006, 14:78–90.

55. Verberk WCEP, van Duinen GA, Peeters TMJ, Esselink H. Importance of variation in water-types for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. In: *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (NEV)*, 2001, 12:121–128.

56. van Kleef HH, van Duinen G-JA, Verberk WC, Leuven RS, van der Velde G, Esselink H. Moorland pools as refugia for endangered species characteristic of raised bog gradients. *J Nat Conserv* 2012, 20:255–263.

57. Brittain J. Life history strategies in ephemeroptera and plecoptera. In: Campbell I, ed. *Mayflies and Stoneflies: Life Histories and Biology*, vol. 44. Dordrecht: Springer Netherlands; 1990, 1–12.

58. Macan TT. *Freshwater Ecology*. 2nd ed. London: Longman; 1974.

59. Foster GN. A review of the scarce and threatened Coleoptera of Great Britain. Part 3: Water beetles of Great Britain, 2010.

60. Hunter D, Osborne W, Smith M, McDougall K. Breeding habitat use and the future management of the critically endangered Southern Corroboree Frog. *Ecol Manage Restor* 2009, 10:S103–S109.

61. Strijbosch H. Habitat selection of amphibians during their aquatic phase. *Oikos* 1979, 33:363–372.

62. Dibner RR, Lawton C, Marnell F. Reproduction of common frogs, *Rana temporaria*, in a managed conifer forest and bog landscape in Western Ireland. *Herpetol Conserv Biol* 2014, 9:38–47.

63. Tuittila E-S, Vasander H, Laine J. Impact of rewetting on the vegetation of a cut-away peatland. *Appl Veg Sci* 2000, 3:205–212.

64. Van Setsers TE, Price JS. The impact of peat harvesting and natural regeneration on the water balance of an abandoned cutover bog, Quebec. *Hydrol Process* 2001, 15:233–248.

65. Poulin M, Rochefort L, Pellerin S, Thibault J. Threats and protection for peatlands in Eastern Canada. *Géocarrefour* 2004, 79:331–344.

66. Stewart AJA, Lance AN. Moor-draining: a review of impacts on land use. *J Environ Manage* 1983, 17:81–99.

67. Coulson JC, Butterfield JEL, Henderson E. The effect of open drainage ditches on the plant and invertebrate communities of moorland and on the decomposition of peat. *J Appl Ecol* 1990, 27:549–561.

68. Wallage ZE, Holden J, McDonald AT. Drain blocking: an effective treatment for reducing dissolved organic carbon loss and water discoloration in a drained peatland. *Sci Total Environ* 2006, 367:811–821.

69. Ramchunder SJ, Brown LE, Holden J. Catchment-scale peatland restoration benefits stream ecosystem biodiversity. *J Appl Ecol* 2012, 49:182–191.

70. Parry LE, Holden J, Chapman PJ. Restoration of blanket peatlands. *J Environ Manage* 2014, 133:193–205.
71. Peacock M, Evans CD, Fenner N, Freeman C. Natural revegetation of bog pools after peatland restoration involving ditch blocking—the influence of pool depth and implications for carbon cycling. Ecol Eng 2013, 57:297–301.

72. Holden J. A grip-blocking overview, 2009.

73. DEFRA. Schmallenberg virus, 2013 Available at: http://www.defra.gov.uk/animal-diseases/a-z/schmallenberg-virus/. (Accessed August 18, 2014).

74. Paffen BGP, Roelofs JGM. Impact of carbon dioxide and ammonium on the growth of submerged Sphagnum cuspidatum. Aquat Bot 1991, 40:61–71.

75. Raghoebarsing AA, Smolders AJP, Schmid MC, Rijnstra WIC, Wolters-Arts M, Derksen J, Jetten MSM, Schouten S, Sinninghe Damste JS, Lamers LPM, et al. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 2005, 436:1153–1156.

76. Beadle JM, Brown LE, Carter CF, Holden J. Saturnus has landed on the moors: first record of Sattus sarrus from the British Isles. FBA News 2014, 63:2–3.

77. Drost MBP, Cuppen HPJJ, van Nieukerken EJ, Schreijer M. De Waterbevers van Nederland. Utrecht: Uitgeverij KNIV; 1992.

78. Biggs J, Williams P, Whitfield M, Nicolet P, Weatherby A. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. Aquat Conserv Mar Freshw Ecosyst 2005, 15:693–714.

79. Belyea LR, Lancaster J. Assembly rules within a contingent ecology. Oikos 1999, 86:402–416.

80. Connor EF, McCoy ED. The statistics and biology of the species-area relationship. Am Nat 1979, 113:791–833.

81. Williams CB. Area and number of species. Nature 1943, 152:264–267.

82. MacArthur RH, Wilson EO. The Theory of Island Biogeography. Princeton, NJ: Princeton University Press; 1967.

83. Scheffer M, Van Geest GJ, Zimmer K, Jepenesen E, Sondergaard M, Butler MG, Hanson MA, Declerck S, De Meester L. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. Oikos 2006, 112:227–231.

84. Oertli B, Joyce DA, Castella E, Juge R, Cambin D, Lachavanne J-B. Does size matter? The relationship between pond area and biodiversity. Biol Conserv 2002, 104:59–70.

85. Larson DJ, House NL. Insect communities of newfoundland bog pools with emphasis on the odonata. Can Entomol 1990, 122:469–501.

86. Johansson F. The slow—fast life style characteristics in a suite of six species of odonate larvae. Freshw Biol 2000, 43:149–159.

87. Verberk WCEP, Siepel H, Esselink H. Applying life-history strategies for freshwater macroinvertebrates to lentic waters. Freshw Biol 2008, 53:1739–1753.

88. Tews J, Brose U, Grimm V, Tiellörker F, Wichmann MC, Schwager M, Jeltsch F. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 2004, 31:79–92.

89. Foster GN, Bilton DT. The aquatic coleoptera associated with patterned mires. In: Standen V, Tallis JH, Meade R, eds. Patterned Mires and Mire Pools: Origin and Development: Flora and Fauna: Proceedings, University of Durham, 6–7 April 1998. London: British Ecological Society; 1998.

90. Fairchild GW, Faulds AM, Matta JF. Beetle assemblages in ponds: effects of habitat and site age. Freshw Biol 2000, 44:523–534.

91. Ribera I, Foster GN, Holt WV. Functional types of diving beetle (Coleoptera: Heteroptera and Dytiscidae), as identified by comparative swimming behaviour. Biol J Linn Soc 1997, 61:537–558.

92. Verberk WCEP, Van Kleef HH, Dijkman M, Van Hoek P, Spierenburg P, Esselink H. Seasonal changes on two different spatial scales: response of aquatic invertebrates to water body and microhabitat. Insect Sci 2005, 12:263–280.

93. Prach K, Walker LR. Four opportunities for studies of ecological succession. Trends Ecol Evol 2011, 26:119–123.

94. Connell JH, Slatyer RO. Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 1977, 111:1119–1144.

95. Chase JM. Drought mediates the importance of stochastic community assembly. Proc Natl Acad Sci USA 2007, 104:17430–17434.

96. Macarthur R, Levins R. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am Nat 1967, 101:377–385.

97. Abrams P. The theory of limiting similarity. Annu Rev Ecol Syst 1983, 14:359–376.

98. Hubbell SP. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton, NJ; Oxford: Princeton University Press; 2001.

99. Verberk WCEP, Van Der Velde G, Esselink H. Explaining abundance–occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. J Anim Ecol 2010, 79:589–601.

100. Van Duinen GA, Verberk WCEP, Esselink H. Persistence and recolonisation determine success of bog restoration for aquatic invertebrates: a comment on Mazerolle et al. (2006). Freshw Biol 2007, 52:381–382.
101. Bilton DT, Freeland JR, Okamura B. Dispersal in freshwater invertebrates. *Annu Rev Ecol Syst* 2001, 32:159–181.
102. Gledhill D, James P, Davies D. Pond density as a determinant of aquatic species richness in an urban landscape. *Landsc Ecol* 2008, 23:1219–1230.
103. Lavers CP, Haines-Young RH. The pattern of Dunlin Calidris alpina distribution and abundance in relation to habitat variation in the Flow Country of northern Scotland. *Bird Study* 1996, 43:231–239.
104. Batzer DP, Wissinger SA. Ecology of insect communities in nontidal Wetlands. *Annu Rev Entomol* 1996, 41:75–100.
105. Clymo RS. Control of cation concentrations, and in particular of pH, in Sphagnum dominated communities. In: Golterman HL, Clymo RS, eds. *Chemical Environment in the Aquatic Habitat*. Amsterdam: Noord-Hollandsche Uitgevers Maatschappij; 1967.
106. Karlsson J, Bystrom P, Ask J, Ask P, Persson L, Jansson M. Light limitation of nutrient-poor lake ecosystems. *Nature* 2009, 460:506–509.
107. Odum HT. Primary production in flowing waters. *Limnol Oceanogr* 1956, 1:102–117.
108. Cornell LP, Klarer DM. Patterns of dissolved oxygen, productivity and respiration in old woman creek Estuary, Erie County, Ohio during low and high water conditions. *Ohio J Sci* 2008, 108:31–43.
109. Coloso JJ, Cole JJ, Hanson PC, Pace ML. Depth-integrated, continuous estimates of metabolism in a clear-water lake. *Can J Fish Aquat Sci* 2008, 65:712–722.
110. Staehr P, Baastrup-Spohr L, Sand-Jensen K, Stedmon C. Lake metabolism scales with lake morphometry and catchment conditions. *Aquat Sci* 2012, 74:155–169.
111. Bunn SE, Boon PI. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. *Oecologia* 1993, 96:85–94.
112. Dai A. Increasing drought under global warming in observations and models. *Nat Clim Change* 2013, 3:52–58.
113. Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. Ecological responses to recent climate change. *Nature* 2002, 416:389–395.
