Relationships between anthropogenic pressures and ecosystem functions in UK blanket bogs: Linking process understanding to ecosystem service valuation

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Quantification and valuation of ecosystem services are critically dependent on the quality of underpinning science. While key ecological processes may be understood, translating this understanding into quantitative relationships suitable for use in an ecosystem services context remains challenging. Using blanket bogs as a case study, we derived quantitative ‘pressure-response functions’ linking anthropogenic pressures (drainage, burning, sulphur and nitrogen deposition) with ecosystem functions underpinning key climate, water quality and flood regulating services. The analysis highlighted: i) the complex, sometimes conflicting or interactive effects of multiple anthropogenic pressures on different ecosystem functions; ii) the role of ‘biodiversity’ (primarily presence/absence of key plant functional types) as an intermediate factor determining how anthropogenic pressures translate into changes in flows of some ecosystem services; iii) challenges relating to the spatial scale and configuration of anthropogenic pressures and ecosystem service beneficiaries; and iv) uncertainties associated with the lags between anthropogenic pressures and ecosystem responses. The conceptual approach described may provide a basis for a more quantitative, multi-parameter approach to the valuation of ecosystem services and the evidence-based optimisation of policy and land-management for ecosystem services.

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1. Introduction

1.1. Rationale

‘Ecosystem services’ provide a basis for the recognition and economic valuation of environmental processes that have beneficial consequences for human wellbeing (Millennium Ecosystem Assessment, 2005). While the approach is now conceptually well developed, its practical application to specific issues and ecosystems remains a challenge. In particular, the effective linkage of scientific process understanding with effective economic valuation and policy presents considerable difficulties, requiring communication between different research communities at an appropriate level of detail (e.g. Carpenter et al., 2009; Seppelt et al., 2011). Without this communication, there is a risk either that scientific knowledge will not be translated into economics or policy, or that economic valuation will proceed on the basis of flawed or incomplete science.

To address this issue, we argue that it is necessary to examine ‘real world’ case studies of specific ecosystems, and to develop effective procedures for distilling complex science into simpler relationships suitable for use by economists. This approach needs to encompass the influence of multiple anthropogenic pressures on ecosystems, the multiple ecosystem services on which these impact, and the geographic context within which these pressures and services operate. Here we focus on peatlands, specifically the blanket bogs of the United Kingdom (UK), as an ecosystem with
recognised importance for a wide range of ecosystem services (e.g. Bain et al., 2011) and with relatively mature associated science on which to base an assessment (e.g. Bonn et al., 2010).

1.2. Status and valuation of ecosystem services from blanket bogs

Peatlands are the largest terrestrial carbon store, despite occupying only 3% of the land surface (Yu et al., 2010). One type of peatland, blanket bog, occurs in areas of high rainfall (usually in maritime climates) with cool temperatures and undulating topography (Lindsay et al., 2010). Blanket bogs are found near the Pacific coast of Alaska, Atlantic Canada, Iceland, the British Isles, Scandinavia, the Faroe Islands, Patagonia and the Falklands, parts of Japan, New Zealand and Tasmania. They are also found in upland environments in New Guinea, Ecuador and Colombia, the Alps and Uganda (Gallego-Sala and Prentice, 2012). Typically blanket peatlands form open landscapes, with a high cover of bryophytes such as Sphagnum, together with vascular plants adapted to high water levels such as bog cotton (Eriophorum), and dwarf shrubs such as Calluna vulgaris in dryer areas. In the UK, peatlands are estimated to hold around 2300 Mt of carbon. Blanket bog is the most extensive peatland type, occupying around 9% of the land surface and comprising over 90% of the UK’s total peatland area (JNCC, 2011; Bain et al., 2011). As well as providing key habitats for rare species, blanket bogs are considered an important part of the UK’s Natural Capital (Robinson et al., 2010) and in good condition can contribute to climate regulation by sequestering atmospheric CO2 via peat accumulation. Due to their position in the headwaters of many river systems, and proximity to major population centres in areas such as Northern England, blanket bogs are also important as sources of clean drinking water (Holden et al., 2007), and as significant contributors to river runoff also have an influence on flood regulation (e.g. Bonn et al., 2010).

Across the UK, and in other parts of the world, blanket bogs have been disturbed by land-use activities, including drainage for grazing improvement, rotational burning to support game bird production, afforestation with non-native conifers, and peat harvesting for fuel or horticultural use. In addition, atmospheric pollutants and wildfires have had detrimental consequences for many blanket bogs, particularly close to population centres (Tallis, 1987, 1997), contributing to the loss of key peat-forming species and ultimately to the onset of peat erosion (e.g. Van der Waal et al., 2011). Although land-use changes have generally been aimed at maximising direct economic benefits (i.e. provisioning services such as livestock, game or timber production), they have tended to be at the expense of the capacity of the peatland to deliver less tangible ecosystem services such as climate, water quality and flood regulation, as well as biodiversity and in some cases amenity value (e.g. Holden et al., 2007; Bonn et al., 2010; Maltby, 2010; Bullock et al., 2012). With increasing recognition of the importance of these services, recent years have seen widespread moves to restore degraded blanket bog, initially with the objective of enhancing biodiversity, but increasingly with complementary aims of improving the climate, water quality and flood regulating capacity of the ecosystem while maintaining direct economic activity (e.g. Bain et al., 2011).

To maximise the ecosystem service benefits of blanket bog restoration, and to create the financial mechanisms that enable those engaged in these activities to realise the societal benefits generated by restoration, there is a need for robust valuations of the ecosystem services provided. These valuations should be based on a strong understanding of the underpinning ecosystem functions (e.g. Cornell, 2010; Maltby, 2010), reflecting the specific ecological characteristics of these systems, and responsive to changes in different anthropogenic pressures, so that the marginal costs and benefits of a change in management (such as restoration) can be accurately quantified (Glenk et al., 2014). Christie and Rayment (2012) derived valuations for conservation-designated bogs in England and Wales based on choice experiments to estimate willingness to pay for a range of ecosystem services, and expert judgement to infer relationships between site management and ecosystem service delivery, which provided valuations in the order of £1000 ha−1 yr−1. For the UK’s National Ecosystem Assessment (NEA), Morris and Camino (2011) provided valuations of a range of ecosystem services associated with freshwater wetlands as a whole. Of the wetland area mapped for the UK in this study, 97% was classified as peat bog, so this wetland type dominated the assessment. Their study valued the regulating service contributions of UK wetlands as follows: flood regulation £608 ha−1 yr−1; water quality regulation £436 ha−1 yr−1; climate regulation (carbon sequestration) £220 ha−1 yr−1. These valuations (per service) were of a similar order to estimated biodiversity and cultural (amenity/recreational) services, and greatly exceeded estimated water supply benefits. The large valuations assigned to wetland regulating services were the source of widely reported ‘headline’ figures from the NEA, including an estimate that UK inland and coastal wetlands provide a total water quality regulating benefit of £1.5 billion per annum (Bateman et al., 2011a). However, the calculations of Morris and Camino (2011) were based on a meta-analysis of international wetland valuation studies (Brander et al., 2006, 2008; EEA, 2010), which incorporated relatively few peatlands. Of the 90 European sites studies used, 10 were obtained from the UK, mostly from lowland fens and other wetlands, and only one from a blanket bog (EEA, 2010).

To summarise, the ecosystem service valuations applied in the NEA to UK wetlands, which are overwhelmingly peat bogs, were derived from a valuation study of international wetlands that overwhelmingly were not peat bogs. The scientific validity of this assessment must therefore be open to question, since the functioning (and thus ecosystem service role) of rain-fed bogs differs fundamentally from other ground-water or surface-water fed wetlands. For example, the water quality regulation function of wetlands considered by Brander et al. (2006) was retention of excess nutrients in groundwater-fed wetlands. While bogs can be effective sinks for atmospheric nutrient deposition (e.g. Bonn et al., 2010; Martin-Ortega, 2014), it is doubtful whether this has the same water quality regulation value as (for example) the retention of diffuse agricultural pollutants by riparian wetlands. Similarly, whereas floodplain wetlands may play a major role in flood attenuation during some times of the year due to their water storage capacity, hilltop blanket bogs are typically sources of flood runoff, and thus their role in flood regulation is very different (Holden et al., 2008). Finally, the assessment of Morris and Camino (2011) which underpinned the NEA valuation study took little account of wetland condition, which as noted above has been strongly impacted by anthropogenic pressures, leading to the degradation of ecosystem service flows. Thus, the robust quantification and valuation of ecosystem services from blanket bogs (as for other ecosystems) requires: 1) a fundamental, ecosystem-specific understanding of their functioning; 2) quantitative information on how different anthropogenic pressures impact on key ecosystem functions; 3) an understanding of how multiple anthropogenic pressures and functions combine or interact; and 4) quantitative information on how changes in ecosystem function translate into changes in the delivery of ecosystem service benefits to the beneficiary population. The majority of published scientific studies of peatlands address point 1. While there is thus a large body of data and process understanding, relatively few studies have specifically (or explicitly) attempted to address points 2 to 4, by developing the simple (i.e. broadly applicable and transferrable),
empirically-based relationships needed for integrated ecosystem service assessment.

1.3. Anthropogenic pressures on UK blanket bogs

In this study, we consider a subset of the most important major anthropogenic drivers of change in UK blanket bogs, namely drainage, managed burning, sulphur (S) deposition and nitrogen (N) deposition (e.g. Van der Waal et al., 2011), and three regulating services identified as having the greatest ecosystem service value for wetlands by the NEA, namely climate regulation, water quality regulation and flood regulation. Of the four anthropogenic pressures considered, drainage and burning can be considered ‘internal’ (management-related) drivers, whereas atmospheric deposition of S and N compounds represent ‘external’ drivers, associated predominately with activities occurring outside the peatland area.

Peatland drainage was extensive across the UK in the 19th century, with the aim of increasing productivity for agriculture, game management or forestry. Although some peat drainage occurred in the 19th and early 20th centuries, this accelerated following the introduction of agricultural subsidies for ditching peatlands in the late 20th century. Following policy changes, far less drainage has occurred over recent decades, although some drainage activity continues associated with, for example, wind farm development. Natural England 2010 estimated that 21% of England’s blanket bogs have been ditched. Drainage may increase agricultural productivity by aerating the peat, providing conditions more suitable for the growth of vascular plants (grasses or heather) but also leading to the mineralisation of stored organic matter (and therefore CO₂ release), as well as impacting on water quality and the timing of runoff (e.g. Holden et al., 2004). Concern about these potentially detrimental consequences, as well as biodiversity loss, has triggered widespread action to restore blanket bogs via the blocking of drainage ditches.

Burning management is practiced across large areas of Northern England and Eastern Scotland, primarily to encourage variable-aged stands of heather, Calluna vulgaris, to support red grouse (Lagopus lagopus) a commercially important game bird. In England, an estimated 30% of blanket bogs is currently subject to rotational burning, of which part is also drained (Natural England 2010). The ecological consequences of managed burning remain contentious, but may include negative impacts on carbon sequestration, biodiversity and water quality (e.g. Van der Waal et al., 2011; Yallop et al., 2010). Conversely, it has been argued that managed burning reduces wildfire risk (Albertson et al., 2009), albeit in managed Calluna-dominated peatlands rather than natural, Sphagnum-dominated systems.

Sulphur deposition, primarily from fossil fuel burning, peaked in the UK during the 1960s–70s. This led to severe acidification of peatlands and other ecosystems, and specifically to the die-back of Sphagnum and other sensitive species in peatlands close to major industrial centres such as the Southern Pennines (Ferguson and Lee, 1983; Tallis, 1987). Sulphur emissions have subsequently declined sharply, but deposition remains above the ‘critical load’ (the maximum dose not considered ecologically damaging) in some areas, and stored sulphur in peatland soils represents a ‘legacy pollutant’ with the potential for remobilisation due to drainage or climate change (Daniels et al., 2008).

Nitrogen deposition is largely associated with emissions from transport and agriculture. As a limiting nutrient it can trigger increased productivity and/or species changes (notably a shift in dominance from peat-forming Sphagnum mosses to vascular plants) in nutrient-poor blanket bogs (Aerts et al., 1992; Berendse et al., 2001). Nitrogen deposition rose during the latter half of the 20th century, and remains high (above the critical load) across many of the UK’s blanket bogs.

1.4. The role of blanket bogs in climate, water quality and flood regulation

Unlike most other terrestrial ecosystems, peatlands can continuously sequester CO₂ from the atmosphere over millennia, leading to the accumulation of large, stable carbon stores in deep layers of waterlogged peat. As a result, blanket bogs now hold most of the UK’s terrestrial carbon store (Billett et al., 2010), and potential rates of carbon loss following anthropogenic disturbance are correspondingly high. In addition, saturated peats are significant sources of methane (CH₄), a potent greenhouse gas with a 100 year Global Warming Potential (GWP, defined as the amount of radiative forcing relative to the same mass of CO₂ over the same time period) of 25 (Houghton et al., 1996). Depending on the relative magnitude of CO₂ uptake and CH₄ emission, peat formation in natural bogs may have either a small net cooling or a small net warming effect. Because CO₂ and CH₄ fluxes respond differently to key environmental drivers, we consider them separately.

‘Water quality’ encompasses a wide range of substances, from man-made chemicals to naturally-occurring substances that, at elevated concentrations, may become ecologically damaging, or present problems for water treatment. It also incorporates physical properties such as water colour and temperature. In rain-fed blanket bogs, most pollution occurs via atmospheric deposition, and water quality regulation occurs via the immobilisation and retention of these pollutants in the peat (e.g. Smith et al., 2012). Agricultural or other catchment pollution sources are usually minor, although they may be significant in intensively grazed areas. Blanket bogs are natural sources of dissolved and particulate organic carbon (DOC and POC), which may be enhanced by some anthropogenic activities, leading to increased water treatment costs. In this assessment we consider the effects of these activities on POC and DOC; a broader evaluation of water quality regulation by peatlands, in relation to the EU Water Framework Directive, is provided by Martin-Ortega et al. (2014).

Blanket bogs generally act as sources rather than stores of flood runoff, due to their characteristically shallow water tables and low water storage capacity (Evans et al., 1999; Price, 1992). Saturation-excess overland flow or near-surface flow dominate water movement (Holden and Burt 2003), enabling rapid water transfer into the drainage network, so that rivers draining blanket bogs tend to have flashy responses to rainfall and high flow peaks. Drainage ditches might be expected to lower water tables and increase storage potential, but also produce rapid flow responses to rainfall because near-surface flow is captured by drains and translated into rapid flow along ditch networks (Holden et al., 2006). Flood regulation can, however, be impacted by surface cover conditions which either slow down (rough vegetated surface) or speed up (bare peat) the velocity of flow (Holden et al., 2008).

1.5. Scope of study

This study aims to provide a ‘worked example’ of the synthesis of complex environmental data, as the basis for more robust ecosystem service assessment and valuation. We attempted to derive a set of quantitative response functions for as many combinations of anthropogenic pressures and ecosystem functions listed above as possible, based on published literature. We also mapped each of the anthropogenic pressures at a national scale, and for one of the ecosystem functions considered (DOC leaching) we applied the response functions obtained for three different scenarios, illustrative of the different anthropogenic pressures experienced by UK blanket bogs from the pre-industrial period through to the present day. The aims of this simulation were both to provide a demonstration of the application of the
While we have attempted to comprehensively and objectively utilise relevant literature and data sources based on the experience and expertise of the authors, we emphasise that this is not a full systematic review or meta-analysis of published literature. Relevant reviews have been undertaken previously (e.g. Bussell et al., 2010; Haddaway et al., 2014), but are limited by the availability of data conforming to the specific requirements of the analysis (e.g. controlled and replicated field-scale interventions), and are rarely able to address multiple stressors and multiple outcomes (i.e. ecosystem functions) simultaneously. Wherever possible we have taken published relationships from comprehensive meta-analyses or multi-site assessments, but for some combinations of environmental stressors and ecosystem responses such comprehensive studies do not exist. In these cases, we have used example relationships from individual studies, or small numbers of studies, and identified these accordingly. In light of this, we emphasise that the relationships and results presented should be considered illustrative rather than definitive. We also recognise that the assessment undertaken here is partial. It focuses on a single habitat type, and on a limited set of associated environmental drivers and ecosystem services. Other anthropogenic activities, such as forestry, grazing and peat cutting, can have profound consequences for peatlands, and the activities considered here also influence other economically important ecosystem services including livestock production, recreational activities and culturally important biodiversity (Bonn et al., 2010). Therefore, our aim here is not to attempt a comprehensive ecosystem service assessment, but rather to begin to define a specific set of ecosystem responses to anthropogenic pressures, following a methodology with the potential for wider application to this and other ecosystem types, based on available data. The approach provides a step towards the more robust quantification and valuation of costs and benefits associated with policy and land-management decisions, supporting the evaluation of co-benefits and trade-offs, and the optimisation of policies to maximise net ecosystem service benefits. By moving beyond a purely conceptual approach, and the initial, relatively coarse valuation of ecosystem services carried out within overview studies such as the NEA (or some ecosystem service models), we hope to provide some generic insights into the methodological challenges, data requirements, pitfalls and possibilities of integrating scientific process understanding for ecosystem service assessment and valuation.

2. Methods

2.1. Derivation of pressure–response functions

To define anthropogenic effects on ecosystem service flows, it is necessary to define an ‘impact pathway’ (e.g. Jones et al., 2011) between the anthropogenic pressure and the ecosystem service of interest. In this study, we followed the impact pathway from the (internal or external) anthropogenic pressure through to its impact on key ecosystem functions, in other words focusing on the fundamental processes that determine the delivery of ecosystem services. To achieve this, we used ‘pressure–response functions’, which are analogous to the dose-response functions used in other fields such as toxicology, and which provide a relatively simple, flexible and empirically-based method for defining this aspect of the impact pathway. The approach aims to derive a quantitative relationship between either the anthropogenic pressure itself (e.g. N deposition rate or burn frequency), or a physically measurable environmental variable that is linked to the anthropogenic pressure (e.g. mean water table depth); and a measurable ecosystem function, such as net carbon balance, that can be used as an input for ecosystem service valuation. Each anthropogenic pressure may impact on multiple ecosystem functions, and each ecosystem function may be affected by multiple anthropogenic pressures.

Fig. 1. Conceptual impact pathway from multiple environmental pressures to the valuation of an ecosystem service. In the illustration shown, each pressure affects a single (beneficial) ecosystem function via a different pressure–response curve. The aggregate effect of these pressures determines the overall level of that ecosystem function, which in turn determines the level of an ecosystem service, and consequently its marginal economic value (in this case assuming a diminishing marginal benefit for each additional unit of ecosystem service, as illustrated for recreational value by Bateman et al., 2011b). Circles show an illustrative ‘present day’ condition. In this example, reducing all three anthropogenic pressures would have synergistic benefits for the ecosystem service, with the greatest marginal benefits obtained by reducing pressures 1 and 3. Conversely, the greatest ecosystem service costs would result from increasing pressure 2.
The conceptual basis of the approach is shown in Fig. 1. The form of pressure-response functions can vary according to the empirical evidence (and its completeness), from simple categorical functions (e.g. drained/undrained) to linear, non-linear or threshold-type functions (cf. Fig. 1). At this stage, we assume that all pressure-response functions are independent, and thus that variations in one anthropogenic pressure do not affect ecosystem sensitivity to another pressure. The practical challenges and limitations of this approach are discussed in Section 4.2.

For each combination of anthropogenic pressures and ecosystem functions considered, we first reviewed available literature to identify whether there was empirical evidence for a causal link. Where a relationship was identified, we attempted to derive continuous pressure-response functions from published studies. Wherever possible, relationships were taken from published meta-analyses or syntheses of data from multiple sites, although this was not possible in all cases. Data specific to blanket bogs were used where available, but often it was necessary to use data derived from (or including) measurements on other peat types. In cases where the available data were insufficient to derive a direct continuous function we used categorical functions (comparable to the ‘export coefficients’ used in some ecosystem service models, e.g. for nutrient retention in InVEST; Tallis et al., 2013), and/or functions based on indirect measures of peatland condition (such as vegetation composition). Full methodological descriptions, data sources and equations describing each of the response functions derived are provided in Section 1 of the Supplementary material. For each of the response functions derived we also assigned a qualitative reliability index based on criteria described in the Supplementary material and summarised in the caption of Table 1.

2.2. Spatial data assessment

As an example of the practical application of the conceptual approach described, we collated data on the spatial distribution of each of the anthropogenic pressures considered for blanket bogs in Great Britain (England, Wales and Scotland) as well as the distribution of potential beneficiaries of peatland ecosystem services. We then applied the response functions derived for one of the ecosystem functions considered, DOC leaching, to examine how these anthropogenic pressures have impacted on ecosystem service delivery at the national scale.

Bog occurrence was obtained from the Centre for Ecology and Hydrology (CEH) Land Cover Map 2007 (Morton et al., 2011), including all 1 km² grid cells containing more than 5% bog habitat. Note that this classification does not distinguish between blanket bog and lowland raised bog, although the former occupies by far the larger area of the UK. Population density was mapped using the density of postcodes (postal administrative units with a mean population of 50 and variable area) as an effective and readily available proxy measure. Managed burn data were obtained from the moorland burn intensity map of Anderson et al. (2009), masked to areas of bog as represented on the LCM 2007 map in order to exclude areas of managed burning on other heathland soils. Spatial data on blanket bog drainage extent are currently available for England only, and were derived from aerial photographic data collated by Natural England for 2008 (Natural England 2010). Areas classified as ‘gripped’, ‘peat-cut’ and ‘extracted’ were included in the drained classification, and the proportion of each grid cell subject to drainage was derived by overlaying the polygon-based Natural England map onto the UK 1 km grid. Gridded total S and N deposition were obtained for the same reference year from http://pollutantdeposition.defra.gov.uk/data, derived from a combination of measurements and modelling by CEH. Again, deposition data were masked to show deposition to grid cells containing > 5% bog habitat.

To examine the combined impacts of drainage, managed burning and S deposition on DOC fluxes, we applied the response functions obtained for each of these pressures for three scenarios, namely: i) a ‘pre-industrial’ baseline state (assuming no peat drainage, management burning or anthropogenic S deposition); ii) the mapped ‘present day’ (circa 2008) levels of each of these pressures; and iii) an illustrative ‘1970s’ scenario representing the period when anthropogenic S deposition was highest, but land-use pressures less intense. In this scenario, we assigned values of S deposition for all grid squares that were three times higher than those observed in 2008 (Mylona, 1996; RoTAP, 2012), and made the simple assumptions that burn intensity was one category lower than that recorded in 2008 for all squares, and drained area 50% lower than that recorded in 2008. Pressure maps and pressure-response functions were then combined for each grid

| Ecosystem service | Ecosystem function | Anthropogenic pressure |
|-------------------|--------------------|------------------------|
| Climate regulation | CO₂ flux | Drainage | Burning | S deposition | N deposition |
|                   | Response function type | Meta-analysis | Single study | Undefined | Multi-site study |
|                   | Confidence level | Continuous | Categorical # | Continuous # |
| Climate regulation | CH₄ flux | Response function type | Meta-analysis | Continuous | Undefined |
|                   | Confidence level | Continuous # | Categorical | Continuous # |
| Water quality regulation | DOC leaching | Source data type | Meta-analysis | Single study | Multi-site study |
|                   | Confidence level | Categorical # | Categorical | Continuous # |
| Water quality regulation | POC leaching | Source data type | Multi-site study | Categorical (based on bare peat area, so indirectly affected by all drivers) |
| Flood regulation | Overland flow velocity | Source data type | Single study | Categorical (based on vegetation cover, so indirectly affected by all drivers) |

* indicates ‘quite reliable’ (based on a limited number of studies), and ‘#’ denotes ‘expert judgement’ (based on few studies, or conceptual understanding).
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cell as follows. The full equations used are provided in the Supplementary material.

1) Runoff xSO₄ concentrations were calculated for each grid cell at each time point by dividing S deposition by 1 km mean discharge concentrations, making the simple assumption that 50% of deposited S is retained in the peat (Evans et al., 2011).
2) The proportion of drained blanket bog was derived for each 1 km grid cell by overlaying the Natural England drainage map.
3) The burning map was used to estimate percentage area of recently burnt blanket bog in each 1 km grid cell, assuming that 33% of the overall area subject to burn management could be classified as recently burnt (based on catchment data presented in Yallop and Clutterbuck, 2009).
4) Pressure-response functions (described below) were aggregated by converting each response function to a ratio relative to the natural baseline, calculating the ratio applicable for each pressure in each grid cell, and multiplying the three ratios obtained to give a single combined ratio.
5) DOC fluxes for each time period were calculated by multiplying this combined ratio with an estimated natural baseline flux of 22 g C m⁻² yr⁻¹ (see Supplementary material) to give a present-day DOC flux.
6) DOC concentrations (which have greater significance for water supply costs than fluxes) were calculated for each time period by dividing the predicted DOC fluxes by gridded runoff estimates (in m yr⁻¹) as used for UK critical load mapping (Hall et al., 2003).

3. Results
3.1. Pressure-response functions
Pressure-response functions derived for the anthropogenic drivers and ecosystem functions considered in the study are summarised in Table 1, and causal relationships represented graphically in Fig. 2. Details on the derivation of response functions (as well as background information on possible relationships for which response functions could not be generated) are given in the Supplementary material. All response functions apply to blanket bog which has not been subject to large-scale land-use change (e.g. afforestation). In total, we were able to define continuous response functions for five combinations of pressure and response variables, and categorical functions for a further three. For POC export and overland flow velocity, response functions were defined relative to intermediate ‘condition’ variables (area of exposed bare peat and vegetation composition respectively), which are likely to reflect the integrated ecosystem response to several anthropogenic pressures. Finally, we were unable to define response functions in four cases, due to either insufficient evidence of effect, or insufficient data to define a relationship.

3.1.1. CO₂ flux response functions
We identified published relationships between CO₂ flux and water table, managed burning and N deposition (Fig. 3). For water table, the empirical relationship obtained by Couwenberg et al. (2011) from a meta-analysis of published studies shows a linear relationship with water table down to at least 50 cm depth, with peatlands acting as a CO₂ sink when mean water table is within 6.5 cm of the surface, and transitioning to an increasing net CO₂ source as water table drops below this threshold. Since it is unusual for water tables to fall more than 50 cm below the surface of blanket bogs, even after drainage, the application of a simple linear response function appears to be justified in this instance. Drain-blocking would be expected to reverse the increase in CO₂ emissions resulting from past drainage.

For managed burning, a simple categorical function (burnt/unburnt) was obtained from a detailed core accumulation study by Garnett et al. (2000) at a replicated, long-term burning experiment in Northern England. Although limited to a single site, the calculated annual C accumulation rate for the unburnt plots was very similar to the accumulation rate estimated for undrained peats by Couwenberg et al. (2011). For the burnt plots, Garnett et al. observed a 73% reduction in C accumulation rate. Equivalent data from other sites would be needed to establish whether this is a consistent response. Clay et al. (2010), working at the same site as Garnett et al., noted an increase in net CO₂ drawdown following burning, counterbalancing for CO₂ loss during burning, suggesting that in reality CO₂ fluxes vary over the burning/re-growth cycle.

Fig. 2. Schematic of impact pathways from anthropogenic pressures to ecosystem services considered for blanket peatlands in the current study. Arrows illustrate type and robustness of pressure-response functions, corresponding to their categorisation in Table 1. Vegetation condition (species composition and cover) is shown as a key intermediate ‘ecosystem state’, which is affected by all pressures and which affects all ecosystem functions; it was specifically used as a predictor for POC loss and overland flow velocity, as shown.
The effects of N deposition on peat C accumulation are complex, due to the transition from growth stimulation of peatland vegetation at low deposition levels, which appears to increase CO2 sink strength (e.g. Turunen et al., 2004), to the displacement of peat-forming plants such as Sphagnum by vascular plants with higher nutrient demands at higher deposition, which will reduce sink strength and could even turn the system into a CO2 source (see Supplementary material for literature and derivation sources of all response functions). The resulting response function is therefore non-linear (Fig. 3c), and is not well defined at higher deposition levels. The enhancement of the CO2 sink by low levels of N deposition is much lower than that reported in forests and heathlands (de Vries et al., 2009), suggesting that any beneficial effects of N deposition for climate regulation by bogs are likely to be negligible at best.

3.1.2. CH4 flux response functions

Emissions of CH4 from peatlands are strongly related to water table, with maximum emissions when water table is close to the surface. Of the two meta-analysis studies used to derive response functions (see Supplementary material) that of Levy et al. (2012), based mainly on data from UK blanket bogs, showed an approximately linear relationship with mean water table down to around 20 cm depth, below which CH4 was near-zero (Fig. 3a). In a separate synthesis of data from continental European peatlands, Couwenberg et al. (2011) observed a similar relationship, specific to sites with aerenchymatous species (higher plants with gas-transporting tissues that act as 'chimneys' for CH4 emission from the water table to the atmosphere). The relationship of Levy et al. (2012) predicts lower fluxes in the water table range 0–20 cm, presumably because the analysis incorporated all vegetation types; Couwenberg and Fritz (2012) also observed lower fluxes relative to water table at sites without aerenchymatous species. The response function of Levy et al. may be most applicable to UK blanket bogs, but a more sophisticated response function, which takes account of vegetation type, could provide more specific predictions, as suggested by Couwenberg et al. (2011) and indicated in a further analysis of UK data by Gray et al. (2013).

There is good evidence that S deposition suppresses CH4 emissions, as sulphate reducing bacteria outcompete methanogenic microbial communities for organic matter substrate. This relationship was quantified by Gauci et al. (2004), who derived an empirical relationship between suppression of CH4 emission and S deposition (Fig. 4b). The relationship is non-linear, with the greatest suppressive effect occurring at low deposition rates.

3.1.3. DOC response functions

We were able to define categorical response functions for DOC leaching relative to drainage and managed burning (Fig. 5a and b). The
drainage response function was based on a previous collation of published DOC studies, which formed the basis for international default ‘emissions factors’ for calculating the contribution of DOC to carbon loss from drained peatlands (IPCC, 2013). The data suggest that drainage increases peatland DOC loss by an average of 60%, sufficient to significantly increase water treatment costs if it occurs in blanket bogs within water supply catchments. Limited available data suggest that re-wetting drained peatlands should reverse this effect (see Supplementary material for a discussion of relevant literature).

For managed burning, we were reliant on a single study by Yallop et al. (2010), which suggests that recently burnt areas of peat export at least twice as much DOC as unburnt areas. In practice, only a small proportion of any area of managed bog will be burnt in any one year, so the impact of burning on DOC losses will be smaller at the catchment scale. The analysis of Yallop et al. (2010) has also been challenged by other authors (see Supplementary material, and Holden et al., 2012 for a review) so this response function is considered to carry a high degree of uncertainty.

For the effects of changing S deposition, we took the empirical relationship published by Monteith et al. (2007) between changes in surface water non-marine sulphate concentration (SO4, considered a proxy for S deposition) and percentage change in DOC concentration (Fig. 5c). The inverse relationship between S deposition and DOC leaching helps to explain the generally lower DOC concentrations observed in UK upland waters during the 1960s–80s peak in S deposition, and their subsequent increase (e.g. Evans et al., 2005). Responses to drainage and burning are thus effectively superimposed on this underlying, externally-driven trend.

3.1.4. POC response functions

POC export is associated with peat erosion (Evans and Warburton, 2007); typical POC fluxes for intact peatlands are <10 g C m⁻² yr⁻¹ (Hope et al. 1997) whilst for severely eroding systems they can exceed 100 g C m⁻² yr⁻¹ (Worrall et al. 2011). POC losses are thus influenced by anthropogenic pressures that lead to exposure of the peat surface or increased overland flow. These potentially include S deposition (causing Sphagnum dieback), fire or overgrazing e.g. Tallis, 1987, 1997; see Supplementary material for further details). On this basis, we derived a simple linear condition response function (Fig. 6) which relates POC loss rates to the proportion of bare peat within an area of blanket bog, based on a collation of peat mass loss data from eroding catchments (Evans and Warburton, 2007). Note that the POC losses from bare peat are of sufficient magnitude to make a major contribution to overall carbon losses from these areas.

The response function shown in Fig. 6 has been tested against measured POC fluxes on a small catchment scale using data from Pawson et al. (2008), Worrall et al. (2003) and Worrall et al. (2011), and was found to predict POC fluxes within the estimated range at 85% of sites, with a significant linear relationship between predicted and observed flux (r² = 0.59). On average the model over predicts fluvial POC flux by 28%, which can be explained by the redistribution of some eroded material within the catchment, suggesting that additional information on the spatial configuration of bare peat areas relative to the drainage network might be used to refine this approach.

3.1.5. Overland flow response functions

Estimates of overland flow velocity were obtained for different characteristic vegetation types from the study of Holden et al. (2008) (see Supplementary material). Velocity data are shown for low and high discharge rates in Fig. 7. The data show that Sphagnum is highly effective at slowing water flow across peat surfaces compared to sedge-covered or bare peat surfaces; flow velocities across Sphagnum were typically almost an order of magnitude slower than for bare peat. Support for a response function based on vegetation condition is provided by recent modelling studies suggesting that surface vegetation cover is likely to be of great importance (more so than the presence or absence of ditches) in the timing of the flood peaks from upland blanket bog.
Grayson et al. (2010) showed, from the hydrograph record of a large blanket peat catchment, that flood peaks were higher during periods when the proportion of bare peat was higher than in periods of more complete vegetation cover. Upscaling the empirical plot-scale equations from Holden et al. (2008) to three UK catchments (Bonn et al., 2010), suggested that changes in both the timing and magnitude of the storm hydrograph peak could be very large if a system moved from 100% bare peat to 100% Sphagnum cover. Promotion of Sphagnum growth by restoration could thus have significant benefits for flood regulation.

3.2. Mapping the spatial distribution of blanket bog, pressures and ecosystem services

The majority of bog habitat (primarily blanket bog) in Great Britain is located in Northern Scotland (Fig. 8a), with smaller (but nonetheless substantial) areas distributed across Southern Scotland, Northern England, Wales and Southwest England. As noted above, this stock of blanket bog may be considered part of the UK’s ‘natural capital’. The distribution of the peat resource is, however, markedly different from that of the UK population (Fig. 8b), much of which is concentrated in the lowland regions of Southern and Eastern England, Central Scotland and South Wales. A key area where blanket bogs and population coincide is Northern England, where large industrial centres lie in close proximity to the blanket bogs of the Pennine uplands. These urban areas receive much of their drinking water from bog-dominated catchments, and the Pennine peatlands are also considered to be of high cultural, landscape and recreational value (e.g. Bonn et al., 2010).

Mapping the four environmental drivers considered (Fig. 9) indicates that the greatest anthropogenic pressures on peatlands often coincide with those regions of high population, where the larger number of potential beneficiaries mean that the level of (spatially dependent) peatland ecosystem services are typically greatest. These spatial relationships are to a substantial degree causative; high levels of S and N deposition to Northern English peatlands derive from the fossil fuel emissions of the urban industrial centres that surround them, which also hold many of the ecosystem service beneficiaries for these peatlands. The spatial distribution of managed burning on bogs is less tightly linked to adjacent population density, but also tends to be greatest in the grouse moors of Northern England, as well those of Southern and Eastern Scotland (Anderson et al., 2009). Although mapping data were not available for blanket bog drainage in Scotland or Wales, data from England show the greatest intensity of drainage within the Northern Pennines, coinciding with high levels of managed burning.

In summary, the greatest ‘natural capital’ of British blanket bogs is located in remote areas of Northern Scotland, where anthropogenic pressures are low. For ecosystem services such as climate regulation that are not distance-dependent, these areas are of high importance. On the other hand, for ecosystem services delivered mainly to nearby
Fig. 9. Spatial distribution and magnitude of the four anthropogenic pressures on blanket bogs considered on bogs, for 2008, masked for 1 km grid cells containing > 10% bog habitat as shown in Fig. 7a. Data shown for a) managed burning (following the burn intensity index of Anderson et al., 2009 as follows: 0 = unburnt; 1 = some burnt fragments; 2 = < 30% of heather burnt; 3 = 30–70% burnt; 4 = > 70% burnt); b) Drainage (as a proportion of each 1 km grid square, based on Natural England peat condition mapping); c) Sulphur deposition (kg S ha$^{-1}$ yr$^{-1}$) and d) Nitrogen deposition (kg N ha$^{-1}$ yr$^{-1}$). Note that peat drainage data were only available for England. For further details of data sources see Section 2.
populations, such as drinking water, flood regulation and recreation, blanket bogs close to population centres such as those of Northern England have a far greater (potential) ecosystem service value per unit area (see also Glenk et al., 2014). However, these areas also tend to have been most degraded by multiple anthropogenic pressures, resulting in erosion, loss of biodiversity, enhanced POC and DOC loss, and reduced overland flow retention. Consequently, these regions can be considered to have the largest ‘ecosystem service deficit’ due to anthropogenic pressures, and thus the greatest potential to enhance ecosystem services through restoration.

In principle, mapped anthropogenic pressures and the pressure-response functions presented above may be combined to generate maps of ecosystem functions, and hence ecosystem service values, as shown in Fig. 1. Reed et al. (2014) describe how such maps and values can be used to prioritise funding via agri-environmental schemes, to incentivise and prioritise land management in locations with the greatest ecosystem service demands and/or ecosystem service deficits. For the worked example presented here, we mapped DOC concentrations in peatland drainage waters across England based on response functions for drainage, burning and sulphur deposition, and for three illustrative scenarios. Since most of the peatland area in England is located in the northern part of the country, Fig. 10 shows results obtained for this area. From Fig. 10a (‘pre-industrial’ scenario), it is clear that (assuming a constant DOC flux across the country) DOC concentrations are naturally higher in lowland raised bogs close to Eastern and Western coasts (> 50 mg l⁻¹), and on the eastern fringes of the central Pennine blanket bog area where runoff is lower (30–40 mg l⁻¹), due to evaporative concentration. Conversely, DOC concentrations are naturally lower (< 20 mg l⁻¹) in high-rainfall western areas of blanket bog. Fig. 10b (‘1970s’ scenario) shows a general tendency towards reduced DOC concentrations, due to the suppressive effects of high S deposition at this time. This is most marked in the more polluted southern part of the study region, close to population centres (see Fig. 8b). Fig. 10c (‘present day’ scenario) suggests that DOC leaching has risen throughout the region following the reductions in S deposition, but suggests an additional increase (beyond the natural baseline) in areas of intensified burning and drainage, particularly in the east of the study region. While these results should be considered indicative, they demonstrate: i) the extent of predicted change in DOC leaching to surface waters due to anthropogenic disturbance of peatland ecosystems; ii) the contrasting effects of different anthropogenic pressures (although note that changes in the pressures considered have tended to have a reinforcing effect over the 1970–2008 period); and iii) the potential to combine pressure maps with response functions to generate spatially explicit predictions of changes in ecosystem function, suitable for input to ecosystem service assessments and valuation studies.

4. Discussion

In this discussion, based on the results of our case study assessment, we consider a number of broader issues associated with the application of a response function approach to defining quantitative links between ecological processes and ecosystem services.

4.1. Pressure-response functions are difficult to quantify

Whilst it is clearly desirable to base response functions on a broad, robust and consistent evidence base, this is rarely straightforward. Different studies use different methods, are often constructed with the aim of detecting a significant (experimental) effect rather than defining a continuous relationship, and rarely cover a spectrum of habitats, soil types and management activities. There is typically a trade-off between breadth of data on one hand (necessitating the use of results from less directly comparable ecosystems, or studies that use somewhat different methods), and the use of the most closely applicable results on the other (which may lead to over-reliance on one or a few studies). As illustrated in Fig. 4a, similar datasets derived from different populations of sites, analysed slightly differently, or subject to different classification or aggregation, may produce different response functions. In this example, the results do appear fundamentally consistent, but highlight the need for careful interpretation and application.

In the examples presented for blanket bogs, we were able to derive continuous (linear or non-linear) response functions for a
number of pressure-response combinations, but could only define simpler categorical functions for others. These equate to the lookup tables used in many existing ecosystem service models, an approach criticised by Seppelt et al. (2009) for relying on coarse and often arbitrary classifications. The need to use a categorical approach was generally a consequence of data limitations, although some anthropogenic activities are effectively categorical in nature (e.g. managed burning either does or does not occur on an area of blanket bog). Furthermore, when categorical functions are upscaled to the landscape (e.g. at the scale of a 1 km grid cell) they may become ‘quasi-continuous’, for example based on the percentage of drained peat within a grid cell. Nevertheless, a more refined approach, e.g. based on intensity of drainage or mean water table depth (as in Fig. 3a and Fig. 4a), may provide more accurate predictions of ecosystem service outcomes.

Finally, we did not consider uncertainties in pressure-response functions in detail, but it is clear that (where quantified, as in Fig. 4a, and Fig. 5a) these may be large. The full assessment of anthropogenic impacts on ecosystem service flows should take account of underlying process uncertainties, and propagate these uncertainties into the economic models used for valuation and cost-benefit analyses.

4.2. Multiple anthropogenic pressures may lead to complex ecosystem responses

Combining multiple anthropogenic pressures in order to predict ecosystem service outcomes is challenging, and we have not attempted to describe a definitive approach here. In the DOC case study presented, we defined a ‘reference’ (natural) DOC flux, and estimated change relative to this baseline assuming that the three pressures were multiplicative, without any interactive effects. In the case of net CO₂ flux (which may be positive or negative, as shown in Fig. 3) it may be more appropriate to treat the combined effect of water table, burning and N deposition as additive. Additional challenges will arise when multiple anthropogenic pressures lead to interactive, non-linear responses. For blanket bogs, examples include the potential threshold effect of N or S deposition as triggers for large-scale vegetation change (e.g. loss of Sphagnum), which could fundamentally alter ecosystem responses (e.g. CO₂ and CH₄ flux, overland flow velocity) to changes in water table or burning regime.

Capturing such complex ecosystem behaviour represents a significant challenge for the empirically-based approaches described here. Defining multi-dimensional response functions for multiple drivers would require complex (and long-term) factorial experiments, with very high associated costs. Survey-based approaches have been used to define empirical relationships between plant species occurrence and a range of environmental variables (e.g. Smart et al., 2010a), and to infer status and change of a range of ecosystem services (Smart et al., 2010b), but again these approaches require very large datasets to capture adequately the effects of multiple drivers on multiple ecosystem services. Finally, as discussed by Reed et al. (2014), the complex ecosystem processes that occur in peatlands may be best described by detailed process models, which are able to incorporate interactions and non-linearities in driver-response relationships. Many ecosystem models incorporate empirically-based functions (e.g. Worrall et al., 2009; Smith et al., 2010; Heinemeyer et al., 2010 for peatlands), so conceptually they may be considered an extension of (rather than an alternative to) the response function approach described here. An analogous approach is used for Kyoto Protocol accounting of land-use derived greenhouse gas emissions, empirically-based Tier 1 (default) and Tier 2 (country-specific) emissions factors to Tier 3 model-based methodologies (IPCC, 2006). Modelling approaches have the potential to describe complex ecological responses to multiple drivers, but may be challenging to parameterise or validate against limited observations. On the other hand, a response function approach provides greater simplicity, transparency and explicit linkages to empirical data, but may fail to capture complex ecosystem behaviour. In practice the two approaches should be considered complementary, and applying them in parallel may provide greater insight into the underlying drivers and overall level of uncertainties in predictions of ecosystem services.

Finally, it is worth noting that lack of complete understanding of complex ecosystem behaviour need not act as a barrier to the valuation of an individual ecosystem service, or to restoration activities intended to enhance it. Even if not all ecosystem services can be quantitatively assessed, our understanding of peatland functioning should be sufficient to target restoration for one service, without causing detrimental effects on other services. The German MoorFutures standard (MLUV M-V (2009), Bonn et al., 2014), like the Verified Carbon Standard (VCS) on peatland related projects, for example, allows for valuation and commodification of climate mitigation services while providing safeguards against losses in biodiversity and socio-economic benefits.

4.3. Lags in ecosystem response to anthropogenic pressures are difficult to capture

Although some ecological responses to anthropogenic pressures may be rapid or even instantaneous, other responses may be subject to significant lags, over periods of years to decades. These lags can occur due to capacity factors, such as the ability of soils to buffer anthropogenic acidification for a period of years, or to accumulate N up to a maximum capacity beyond which leaching and eutrophication occur. Alternatively, they may be associated with decreased ecosystem resilience to acute natural or anthropogenic pressures, e.g. drainage may reduce peat susceptibility to drought, triggering species changes, CO₂ loss and erosion. Conversely, ecosystem recovery following the reduction or removal of an anthropogenic pressure may be lagged, leading to hysteresis in the pressure-response function. An extreme example of this is the onset of gully erosion in the Southern Pennines of England, which although thought to be triggered by air pollution and over-intensive land-management during the mid-20th century, may be effectively irreversible without large-scale intervention through gully-blocking and revegetation. In some cases, restoration activity could even have a transient negative effect on other some ecosystem functions, as in the case of the ‘spike’ of methane emissions which has been observed in the early stages following peat re-wetting (Tuittila et al., 2000; Cooper et al., 2014).

In many cases, lags between anthropogenic pressures and ecosystem responses are associated with changes in vegetation composition, particularly the presence or absence of key plant species or functional types. While ‘biodiversity’ is often recognised as an end-point of ecosystem service assessments, with considerable ongoing work to incorporate the biodiversity concept within valuation studies (e.g. Christie and Rayment, 2012; Helm and Hepburn, 2012; Atkinson et al., 2012), equally the role of biodiversity or its constituent components is seen to be a critical influence on the ecosystem functions that determine ecosystem service flows (Cardinale et al., 2012; de Bello et al., 2010). A partial solution to the issue of lags between anthropogenic pressures and ecosystem responses is to define ‘condition-response’ functions, whereby the characteristics of the ecosystem which dictate ecosystem function (such as vegetation composition as a control on GHG flux or overland flow, or bare peat area as a control on POC loss) are used in preference to the original anthropogenic pressures. This approach (as used in Figs. 6, and 7) has the advantage of being more tightly linked to mechanisms, and implicitly takes account of lags
ecological responses. Condition-based measures may also (as in the examples above) be more conducive to measurement and reporting, via ground-based or airborne monitoring of vegetation or other readily-observable characteristics (e.g. Couwenberg et al., 2011; Bonn et al., 2014). On the other hand, condition-based methods are less closely connected to the original anthropogenic pressure(s), and the impact pathway from policy/management change through to ecosystem service benefit may therefore be more difficult to define. For example, ecosystem functions that are influenced by plant species composition may be determined by the integrated response of the plant community to the combined effects of drainage, burning and atmospheric deposition over a period of decades. Where lags are important, a more complex modelling approach may therefore be required.

4.4. It is rarely possible to capture all ecosystem services

In the case study presented here, we focused primarily on regulating ecosystem services provided by blanket bogs. We did not quantify either the direct economic benefits of peatland-management activities such as farming or grouse-rearing, or the more intangible cultural service benefits associated with (for example) the landscape or biodiversity value of blanket bogs in differing condition, or their role in sustaining neighbouring rural communities. Our consideration of regulating services is in itself partial; for example, while blanket bogs do not retain agricultural nutrients to anything like the extent suggested in the valuations assigned to UK wetlands by the NEA (Morris and Camino, 2011), good condition bogs are effective at retaining atmospheric pollutants including nitrogen, metals and persistent organic pollutants (Bonn et al., 2010; Martin-Ortega et al., 2014), with consequent benefits for aquatic biodiversity and water supplies. While we were not attempting here to undertake a full ecosystem service assessment, these examples serve to demonstrate the breadth and complexity of the functions performed by blanket bogs, and the challenges inherent in attempting a comprehensive valuation or cost-benefit analysis. Clearly, an assessment focusing on only a subset of ecosystem services risks presenting a distorted view of their role, and may lead to non-optimal policy or management decisions. Nevertheless, our current understanding of peatland ecosystem services allows us to provide guidance on management options to enhance certain services while preventing harm to others.

5. Conclusions

This study has focused on developing a conceptual framework for characterising and quantifying the relationships between anthropogenic pressures and the ecosystem functions that deliver ecosystem services. As illustrated by Fig. 1, a sound scientific underpinning is a vital first stage in any ecosystem service valuation, without which the valuations obtained (and subsequent decision-making) risk being incomplete or inaccurate. By linking our assessment to the economic valuation of ecosystem services (Glenk et al., 2014) and the design of agri-environment schemes (Reed et al., 2014) in the same case study ecosystem, we have attempted to bridge the gap between scientific and socio-economic assessment of ecosystem services. Based on the outcome of this case-study, we draw the following conclusions regarding the incorporation of scientific process understanding in valuation studies:

- Ecosystem service valuations should take account of the effects of multiple anthropogenic pressures. Our analysis illustrated that both local management activities and larger-scale ‘external’ pressures can affect ecosystem service delivery. In some cases different pressures can have opposing effects on the same ecosystem function (e.g. sulphur deposition and drainage effects on DOC loss) and in some cases the same driver can have opposing effects on different ecosystem functions (e.g. drainage effects on CO₂ and CH₄ emissions). Scientific process representation (via response functions or models) should be sufficiently simple and transparent to permit quantitative analysis of the full impact pathway from anthropogenic pressure to economic outcome, based on realistically available data. Our assessment showed that, even for comparatively well-studied blanket bog ecosystems, the derivation of response functions is often data-limited.

- Relationships between anthropogenic pressures and ecosystem functions, as well as ecosystem service valuations, should be based on empirical data for that ecosystem, preferably from multiple studies. Transferring relationships from ostensibly similar ecosystems (e.g. from riparian wetlands to blanket bogs) may lead to erroneous valuations and policy responses.

- In light of these issues, there is a clear need for scientific studies to generate and report results in a form suitable for translation into meta-analyses, response functions and models for ecosystem service assessment.

- Subject to the availability of adequate empirical data, future development of the response function approach should take account of interactions between drivers, scale issues, non-linearities, time lags and potential hysteresis in the relationships between pressures and ecosystem responses.

- Data used to characterise anthropogenic pressures and ecosystem condition should (as far as possible) be spatially explicit, as should data on the distribution of ecosystem service beneficiaries. This will enable the cost-effective targeting of policies and payment schemes towards areas where potential for ecosystem service gains is greatest. Our study indicated that UK peatlands areas with the greatest current ecosystem service deficits were also those with the highest density of potential beneficiaries in nearby urban areas, making these prime areas for restoration.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.ecoser.2014.06.013.

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