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1 **Title: Methane Indicator Values for Peatlands: a comparison of species and functional**
2 **groups**

3 Running Title: *Peatland methane indicator values*

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3

1 Abstract (300)

2 Previous studies have shown a correspondence between the abundance of particular plant
3 species and methane flux. Here we apply multivariate analyses, including a weighted
4 averaging approach, to assess the suitability of vegetation composition as a predictor of
5 methane flux. We developed a functional classification of the vegetation, in terms of a
6 number of plant traits expected to influence methane production and transport, and compared
7 this with a purely taxonomic classification at species-level and higher. We applied both
8 weighted averaging and indirect and direct ordination approaches to six sites in the UK, and
9 found good relationships between methane flux and vegetation composition (classified both
10 taxonomically and functionally). Plant species and functional groups also showed meaningful
11 responses to management and experimental treatments. In addition to the UK, we applied the
12 functional group classification across different geographical regions (Canada and
13 Netherlands) to assess the generality of the method. Again, the relationship appeared good at
14 the site level, suggesting some general applicability of the functional classification. The
15 method seems to have the potential for incorporation into large-scale (national) greenhouse
16 gas accounting programmes (in relation to peatland condition/management) using vegetation
17 mapping schemes. The results presented here strongly suggest that robust predictive models
18 can be derived using plant species data (for use in national-scale studies). For trans-national-
19 scale studies, where the taxonomic assemblage of vegetation differs widely between study
20 sites, a functional classification of plant species data provide an appropriate basis for
21 predictive models of methane flux.

1 **Introduction**

2 Methane (CH₄) is a potent greenhouse gas, and emissions from peatlands account for a large
3 proportion of the global total emissions, although, there is considerable uncertainty about
4 their magnitude (Billett *et al.*, 2010, Conrad, 2009, Petrescu *et al.*, 2010). Peatland CH₄
5 emissions may be expected to rise under warmer and wetter climate change predictions, and
6 in response to practices such as peatland restoration and re-wetting (Denman *et al.*, 2007,
7 Waddington & Day, 2007). It has been proposed that by changing peatland management,
8 both a reduction in greenhouse gas emissions and positive outcomes for biodiversity can be
9 achieved (Bain *et al.*, 2011). In addition, policy-makers require simple emission factors that
10 are responsive to the effects of land management activities in order to account for the net
11 emission of greenhouse gases but as yet, these are in the early stage of development
12 (Couwenberg *et al.*, 2011).

13 CH₄ fluxes are usually measured at small scales (often <1m²) over a period of minutes using
14 chamber methods, and less frequently at larger scales (<1 km²) by eddy covariance. There are
15 considerable difficulties in extrapolating these measurements to annual estimates at regional,
16 national, or global scales but the data are often used to parameterise CH₄ emission models
17 (Arah & Stephen, 1998, Smith *et al.*, 2007, Walter & Heimann, 2000, Zhang *et al.*, 2012).

18 Most commonly, a process-based model is used, which attempts to represent the responses of
19 methane production and oxidation to temperature, soil moisture, water table levels, anaerobic
20 state, pH, substrate concentrations, and other environmental factors deemed important (Arah
21 & Stephen, 1998, Smith *et al.*, 2007, Walter & Heimann, 2000). However, our
22 understanding of the responses of the different microbial taxa involved to environmental
23 variables is imperfect (Conrad, 2009). Furthermore, the correspondence between the
24 environmental variables measured in the field and those which actually drive CH₄ production

1 and oxidation is often not as good as would be desired. For example, Levy *et al.*, (2012)
2 found that environmental variables explained only 50 % of the variance in instantaneous CH₄
3 chamber flux measurements, although this was improved after temporal and spatial
4 averaging.

5 As an alternative or complementary approach, vegetation species composition provides a
6 long-term integrator of environmental conditions, and some studies have shown the potential
7 to use this to explain or predict CH₄ fluxes (Bubier *et al.*, 1995, Dias *et al.*, 2010). Bubier *et*
8 *al.*, (1995) examined bryophytes as predictors of methane flux and found them to be good
9 surrogates for the degree of anaerobism/aerobism in two peatlands in Canada. In two
10 peatlands in the Netherlands, Dias *et al.*, (2010) found that both vascular and non-vascular
11 species composition are good predictors of methane flux. The use of vegetation-based proxies
12 have been proposed as a basis for large-scale peatland greenhouse gas flux accounting by
13 Couwenberg *et al.*, (2011). However, this approach requires testing on a much wider scale to
14 assess its applicability and generality. Because plant species data are widely available, if a
15 robust relationship could be established between CH₄ fluxes and vegetation, this may provide
16 an effective indicative tool for CH₄ fluxes to larger scales and for national-scale inventories.

17 Despite the demonstrated importance of plant species for CH₄ emissions, taxonomically
18 defined species may not be the best approach for reflecting CH₄ emissions. This is because a
19 natural species classification seeks to classify organisms in terms of their evolutionary
20 relationships rather than with respect to their influence on biogeochemical processes. In
21 addition, to make comparisons across regions a common framework is required. However,
22 species pools differ from region to region and hence a taxonomic classification may not be
23 the best basis as methane indicators. A solution to this problem might be to classify species
24 into functional groups; this approach has been applied several times in peatland systems (e.g.

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1 Backstrand *et al.*, 2008, Baird *et al.*, 2009, Ward *et al.*, 2009). These would ideally reflect the
2 function-process-vegetation relationship and be sensitive enough to demonstrate responses to
3 changes in environmental conditions. However, defining a functional group in peatlands can
4 be problematic simply because quantitative trait data are absent for many peatland vascular
5 species and the majority of bryophytes. On the other hand, comparable qualitative attribute
6 data for both vascular plants and bryophytes have been collated for the UK (Hill *et al.*, 2007,
7 Hill *et al.*, 2004). This offers the possibility of defining an *a priori* set of plant attributes that
8 relate to CH₄ flux, such as the possession of aerenchyma (air channels that allow gaseous
9 exchange between the shoot and the root) or the association of methanotrophic bacteria with
10 *Sphagnum* species (Raghoebarsing *et al.*, 2005). In addition to the fact that plant species
11 respond to the same environmental factors that influence CH₄ emission, it also has been
12 shown that plants can have a direct effect on CH₄ production and emission (Aulakh *et al.*,
13 2001, Joabsson *et al.*, 1999, Shannon *et al.*, 1996).

14 Levy *et al.*, (2012) analysed nearly 5000 chamber measurements of CH₄ flux from 21 sites
15 across the UK. They found that less than half of the observed variability in instantaneous
16 fluxes could be explained by independent variables measured but where plant species
17 composition data were available, this provided the highest explanatory power. Here, we
18 extended the analysis of Levy *et al.*, (2012) by adding further data from sites where plant
19 species composition has been determined. We applied a “weighted averaging” approach to a
20 range of sites in the UK, as well as continental Europe and Canada. To enable a degree of
21 generality across continents where the degree of species overlap is incomplete, species were
22 classified into functional groups. These are defined by a number of qualitative traits related to
23 species responses to environmental factors that also control CH₄ emission and to direct
24 effects of plant species on CH₄ emission. We compared the results based on this functional

- 1 classification with those based on the original species composition data using a purely
- 2 taxonomic classification.
- 3

1 **Materials and Methods**

2 *Site Descriptions*

3 The measurements analysed here were made at sites in Scotland, Wales and England in the
4 U.K. (Table 1). These peatland sites are all characterised by high water table levels and
5 acidic deep peat; further site specific details can be found in Table 1 and elsewhere (Billett *et*
6 *al.*, 2010, Carfrae *et al.*, 2007, Dinsmore *et al.*, 2009, Gray, 2006, Ward *et al.*, 2007). Two
7 sites have plots located in a designed experiment (Whim and Moor House: nitrogen; burning;
8 grazing) and the rest of the plots are located within sites on a range of different management
9 practices (remaining sites: drainage; grazing; burning).

10 *CH₄ flux measurements*

11 At each site CH₄ fluxes were measured using a similar measurement procedure. A cylindrical
12 PVC collar was inserted into the soil and left in place for a number of weeks or months. On
13 each sampling occasion, a lid was sealed on top, and left in place for up to 2 h, but more
14 commonly 30 min to 1 h. Samples were removed by syringe through a 3-way tap or rubber
15 septum, and analysed on a gas chromatograph, together with replicates of three or four
16 standard gases with known concentrations. For each sequence of gas samples from a
17 chamber, the flux ($\text{mol m}^{-2} \text{s}^{-1}$) was calculated as the rate of change in concentration (mol
18 mol^{-1}) with time (s), by linear regression; taking into account the density of air, chamber
19 volume, and surface area. At most of these sites, measurements were made approximately
20 monthly over one or more years, covering all seasons. Where there are important differences
21 in methodology (chamber size, gas sampling method etc.), these are detailed in Table 1 of
22 Levy *et al.*, (2012). Full details of the methods used can be found elsewhere (Billett *et al.*,
23 2010, Carfrae *et al.*, 2007, Dinsmore *et al.*, 2009, Gray, 2006, Ward *et al.*, 2007).

1 *Vegetation Sampling*

2 At each site vegetation composition was assessed as percentage cover by species for vascular
3 plants, bryophytes, macro-lichens and bare peat from within each of the CH₄ chambers
4 except at Moor House. At Moor House vegetation was averaged from three randomly located
5 quadrats within each treatment plot; deriving a mean cover for each treatment. Cover was
6 assessed from the chambers located in Wales (Migneint) from photographs with species
7 identification confirmed from voucher specimens. All percent cover values were converted to
8 the ten point DOMIN scale (sensu Dahl and Hadač (1941) see Rodwell, 1991a) prior to
9 analyses.

10 *Functional Classification*

11 De Deyn et al., (2008) suggest a trait base approach to plant classification in relation to
12 carbon. However, in bryophyte dominated systems such as peatlands, quantitative plant trait
13 data are not yet widely available. We therefore use a systematic approach to define functional
14 groups from qualitative characteristics that we expect to have a relationship to CH₄ fluxes;
15 these attributes are defined in Table S1. Most of the attributes are taken directly from Hill et
16 al., (2004) for vascular species and Hill et al., (2007) for bryophytes, however, there were
17 some exceptions to this. For *Sphagnum* spp., life forms were derived to reflect a microhabitat
18 classification with the assumption that this has a close relationship to water table depth.
19 Vascular plants were classified as possessing aerenchyma from literature sources or this was
20 assumed in the absence of evidence but where strong habitat association exists i.e. those
21 known to inhabit inundated sites. We also include a literature derived nitrogen fixation
22 classification. Functional groups were classified such that groups of species that have the
23 same life form, woodiness, aerenchyma and N fixation, comprise the same functional group
24 (Table S2). The following serve as examples: *Myrica gale* is functionally coded “PnwAAct”

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1 meaning it is a nanophanerophyte (Pn), woody (w) , possesses aerenchyma (A), and has an
2 actinorhizal nitrogen fixation relationship (Act); *Hylocomium splendens* and *Pleurozium*
3 *schreberi* are both coded “Weh” having a weft life form (We) and being herbaceous (h);
4 *Sphagnum capillifolium* and *S. fuscum* were coded “HumhCya” meaning hummock form
5 (Hum), herbaceous (h) and likely to harbour N fixing cyanobacteria (Cya). An additional
6 standalone type was also used for bare peat; ultimately the 135 different species recorded
7 from the UK, Canadian and Netherlands sites were arranged into 20 functional groups.
8 Abundance data were summed for each functional group.

9 *Data Analysis*

10 Vegetation data were first analysed by Detrended Correspondence Analysis (DCA) to
11 determine the correlation between the first axis and log mean CH₄ emissions, entered as a
12 passive variable; additionally site was also included as a passive variable. We then performed
13 a Canonical Correspondence Analysis (CCA) to determine the relationship between
14 species/functional groups and the experimental/management treatments. Due to the
15 differences in methodology between sites, site was included as a co-variable. As with DCA,
16 CH₄ emissions were included as a passive variable. Both these analyses were carried out
17 using Canoco 4.5 and Canodraw 4.1 software (ter Braak & Šmilauer, 2002).

18 Models to derive predictions of CH₄ flux were developed using weighted averaging (WA)
19 regression as in Bubier et al., (1995) and Dias et al., (2010). WA assumes a unimodal
20 response of species to a certain environmental variable. This means that species have their
21 maximum abundance at their optimum position along the environmental gradient. Although,
22 plants do not respond directly to CH₄ fluxes nor have an optimal CH₄ flux in any biological
23 sense, but the terms optimum and tolerance are retained for consistency with the literature on
24 gradient analysis. As our approach is analogous to Bubier et al., (1995) and Dias et al.,

1 (2010) we refer the reader to these publications, and in addition, ter Braak and Barendregt
2 (1986), Jongman *et al.*, (1987), Birks *et al.*, (1990) and ter Braak and Juggins (1993) for
3 specific details of the WA methodology. The WA species optima are calculated as an average
4 of the CH₄ flux weighted by species abundance and that these optima, together with species
5 abundance, are used to predict fluxes. To account for the prediction of extreme values we use
6 only the classical deshrinking procedure as inverse deshrinking gave very similar results (see
7 Birks *et al.*, 1990, Osborne, 1991, ter Braak & Barendregt, 1986, ter Braak & van Dam,
8 1989). The deshrinking procedure corrects the inherent bias toward the median of the
9 observed range, resulting from taking averages twice during WA reconstitution: once in WA
10 regression and once in WA calibration (see also Bubier *et al.*, 1995)

11 To explore the predictive ability of the WA technique a 70/30 split of the data was used to
12 perform cross-validation; for each WA model a completely random selection without
13 replacement of 30% of the vegetation stands were left out in turn for all possible
14 combinations. The WA function from the selected vegetation stands was then applied to the
15 omitted ones, giving for these plots a prediction and an error prediction.

16 Finally, our approach to functional group classification was applied to the datasets from
17 Bubier *et al.*, (1995) and Dias *et al.*, (2010). Here the species were grouped in the same way
18 as detailed above; functional classifications for each of the species included can be found in
19 the supporting material (Table S2). As neither Bubier *et al.*, (1995) nor Dias *et al.*, (2010)
20 give species abundance data, we used the published optima to derive a median value for each
21 functional group and taxonomic family for use in the WA calculations. We confine our
22 comparison to family and functional groups as there was as no abundance data for assessing
23 dominant species and as Bubier does not include any vascular species so it was not possible
24 to include aerenchymatous species. Nevertheless, by using the same approach with our larger

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- 1 dataset from our sites, a comparative evaluation of the success of our functional classification
- 2 outwith the UK was made.

1 **Results**

2 The DCA analysis showed a negative correlation between axis one and CH₄ emission in both
3 species (-0.54) and functional group (-0.50). This indicates a strong relationship between the
4 variance in species or functional group and CH₄ emission. The variation explained by axes 1
5 and 2 for the species and function group data was 15.9% and 29.2% respectively. As
6 expected some species/functional groups/species are more correlated than others to CH₄
7 (Figure 1).

8 Monte Carlo permutations of the canonical correspondence analysis (CCA) of the species
9 data set showed that axis 1 (eigenvalue of axis 1 = 0.174,) and all axes (sum of all axes
10 canonical eigenvalues = 0.480) were significant ($p < 0.01$). The cumulative percentage
11 variance explained by all axes of the species data was 9.7% and of the species-environment
12 relation was 76.2%. Axis 1 and 2 were more strongly correlated with grazing treatments than
13 other treatments. A similar pattern was evident in the functional group dataset the canonical
14 correspondence analysis (CCA) showed that axis 1 (eigenvalue of axis 1 = 0.119,) and all
15 axes (sum of all axes canonical eigenvalues = 0.272) were significant ($p < 0.01$). The
16 cumulative percentage variance explained by all axes of the species data was 16.1% and of
17 the species-environment relation was 36.3%. Axis 1 and 2 were again more strongly
18 correlated with grazing treatments than other treatments. In both species and functional group
19 analyses CH₄ emissions were most highly correlated to axis 3 but the correlation was weak
20 (0.2 in both cases); the highest treatment correlation with axis 3 was a positive correlation to
21 burning (spp: 0.39; FG: 0.25) and negative to drainage (spp: -0.32; FG: -0.27).

22 Functional group appear to have a slightly narrower range of WA optima than species (Spp. –
23 0.5 to 1.6; FG - 0.9 to 1.4), in addition species also appear to have wider tolerance (Figure 2).
24 Species also have a propensity to be less widely distributed, for example, the highest WA

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1 optima for species are associated with *Vaccinium oxycoccos* (1.6) and *Sphagnum*
2 *magellanicum* (1.6) and lowest WA optima with *Deschampsia flexuosa* (0.5) and *Festuca*
3 *ovina* (0.5); these species only appear in one site Whim, Forsinard and Auchencorth
4 respectively. In comparison the functional group members are likely to be more widespread
5 for instance *LawnhCya* occur in 2 sites, *bare peat* in 3 sites, *hch* in 2 sites and *tfh* in 5 sites.

6 The WA optima (Figure 2) for species and functional groups allowed reliable predictions of
7 CH₄ fluxes based on both cross validation (Table 2) and the complete dataset (Figure 3a-h).
8 Changing the spatial resolution from individual sites to sub site, treatment and plot levels
9 decreases the predictive power as shown by decreases in r square (adjusted) values (Figure
10 3). On the whole, functional groups appeared to be slightly better in linear predictive power (r
11 squared) than taxonomic classification, species/family. However, the root mean squared error
12 (RMSE) tended to be slightly higher for functional group than in species suggesting a better
13 1:1 relationship for taxonomic classification such as species (Table 2 and Figure 3a-h).

14 We found two published studies (Bubier *et al.*, 1995, Dias *et al.*, 2010) where there was plant
15 species data to allow our functional group classification to be applied and the original
16 correlation between species CH₄ WA predictions and observed CH₄ was good. The
17 predictions based on WA calculated for our functional group classification for these studies
18 showed good agreement with the published observed CH₄ fluxes (adj r² = 87.7). When WA
19 predictions are plotted for all sites including the additional published sites against the
20 observed values the r-squared (adjusted) is very high (0.87) and close to a 1:1 fit (WA CH₄ =
21 - 8.823 + 1.796 Observed CH₄) (Figure 4). However, when using the family classification the
22 correspondence between observed and predicted was poor (adj r² = 2.7).

1 **Discussion**

2 The low percentage of variance explained in the unconstrained ordination analyses here is
3 due to the presence of many zero values in the data, and is typical for such noisy data sets
4 representing long environmental gradients (*c.f.* Bubier, 1995). Nevertheless, significant
5 relationships were detected for both species and functional groups in the constrained analyses
6 in relation to land management practices and experimental treatments. Species tend to show a
7 better correlation with the explanatory variables than functional groups. However, both
8 classifications were significant. This serves to underline the evidence that practices such as
9 grazing, drainage, burning and nitrogen manipulation can have a strong influence on species
10 and thus functional group composition (e.g. Carfrae *et al.*, 2007, Cooper *et al.*, 2001, Grant *et*
11 *al.*, 1976, Gunnarsson, 2000, Hobbs, 1984, Kuhry, 1994, Marrs *et al.*, 2004, Rawes &
12 Hobbs, 1979, Stewart & Lance, 1991). The WA method appears to work well for explaining
13 variance in observed mean CH₄ using either taxonomic or functional classifications. Bubier
14 (1995) used the same technique and reported similarly high r^2 values using on bryophyte
15 composition data. Again using WA, Dias *et al.*, (2010) also reported good relationships
16 though with slightly lower r^2 (0.47 - 0.67; derived from the published r values) for the fit
17 between vascular and non-vascular species WA predictions and observed CH₄ fluxes.

18 The increase in variance explained with increasing spatial scales from plot-
19 level/treatment/sub-site /site is in accordance with the findings of Levy *et al.*, (2012). Possible
20 reasons for this were discussed at length in Levy *et al.*, (2012) e.g. random measurement error
21 in the flux and/or independent variable data, cancelling out as more measurements are
22 averaged. However, one additional source of random measurement error here is the
23 unaccounted observer error in the plant abundance data, although, the use of the DOMIN
24 scale and including site as a co-variable in the ordination should compensate for this to some

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1 extent.

2 Methane flux has frequently been related to abiotic variables such as temperature (Kettunen
3 *et al.*, 2000, Laine *et al.*, 2007, MacDonald *et al.*, 1998), and water table levels (Liblik *et al.*,
4 1997, MacDonald *et al.*, 1998) and this approach frequently forms the basis of process
5 models (e.g. Smith *et al.*, 2007). In an analysis of a large UK dataset, Levy *et al.*, (2012)
6 found that when spatial and temporal variation were controlled, up to ~75 % of the variance
7 in CH₄ fluxes could be explained. Soil carbon, peat depth, soil moisture and pH together
8 provided the best sub-set of explanatory variables. However, for the three sites where plant
9 species composition data were available, this provided the highest explanatory power (Levy
10 *et al.*, 2012). Plant species composition is less routinely examined than environmental
11 variables such as water table levels or temperature but there is increasing evidence of their
12 power as an indicator of methane flux. In a UK bog (Greenup *et al.*, 2000) and in Germany
13 (Couwenberg *et al.*, 2011) good relationships were evident between aerenchymatous species
14 and CH₄ emission. In contrast we found weaker relationships with aerenchymatous species
15 than either all plant species or our functional groups. We suspect this is because
16 aerenchymatous species are only showing one functional response and there are likely to be
17 multi-functional responses that promote or decrease methane flux with regard to
18 anaerobic/aerobic decomposition processes. Strong correlations between the emission of CH₄
19 and bryophytes abundance were found in Canada (Bubier *et al.*, 1995) that were indicative of
20 long term water table levels and temperature regimes. In the Netherlands, good agreement
21 between plant species composition and methane flux were detected (Dias *et al.*, 2010) again
22 directly related to water table level. The data examined here add to this evidence and
23 indicates that both species and functional groups appear to be good predictors of methane
24 flux. Nevertheless, the previous analyses (Levy *et al.*, 2012) suggests that plants may not
25 always have simple relationships to long term water table level and temperature and that

1 other mechanisms may be responsible. That said, there still seems to be good potential for
2 either species or functional groups to be indicators of methane flux. Species and higher
3 taxonomic classifications tended to show a slightly better 1:1 relationship with predicted and
4 observed CH₄ emissions as indicated by lower RMSE values but higher r^2 were found for
5 functional groups. Nonetheless, if plant composition is to be used to predict or indicate
6 methane flux on wider spatial scales then it would seem that a functional group approach may
7 have a reasonable predictability and wider geographic applicability than species.

8 That the functional classification applied here is at least as good (in terms of r^2) as the
9 taxonomic classification is encouraging. It also suggests that the classification of functional
10 groups used here captures to some extent the function-process-vegetation relationship and is
11 somewhat sensitive to responses to disturbance. In addition, the functional group
12 classification gives generality to the method spanning multiple sites and regions, as
13 demonstrated by the application to the Canadian and Dutch data. As the total number of
14 species involved in larger scale studies can be quite large the use of functional groups
15 addresses the problem of some species being isolated to single sites or regions. By
16 aggregating species into functional groups this become less of a problem without the loss of
17 explanatory power.

18 To improve this approach it would be useful to evaluate whether the functional characteristics
19 used here are the most appropriate. Quantitative traits (see e.g. De Deyn *et al.*, 2008) with
20 more 'biogeochemical' characteristics may be a more appropriate for classifying functional
21 groups (e.g. foliar C/N ratio, annual growth rate, below and above ground biomass ratio,
22 rooting depth, quantitative assessment of labile substrate production for methanogenesis etc.)
23 and traits related to the response to environmental factors that also control CH₄ flux (such as
24 water table level and N availability). However, at present these cannot be defined for many

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1 species across a range of taxa, particularly bryophytes, as pertinent data are lacking. Further
2 refinements to improving this approach need co-located datasets of both CH₄ flux and
3 vegetation from broad geographical scales (different countries and continents). These data
4 would give a more comprehensive testing of the WA and functional group approaches
5 proposed here and assess its applicability on a global scale.

6 The obvious potential strength of a vegetation indicator approach is that by using species or
7 functional group abundance there is the potential for indicative fluxes to be mapped. For
8 example, from data commonly gathered for vegetation mapping programmes such as the
9 National Vegetation Classification or Countryside Survey (NVC; CS) in the UK (Rodwell,
10 1991b) or Corine Biotope mapping in Europe (Moss *et al.*, 1991) or national vegetation
11 classification in Northern America (Grossman *et al.*, 1998) one could potentially derive
12 methane flux indicator values for plant communities from species or functional group. In
13 addition, it may also be possible to assess the effects on methane flux indirectly through
14 examining vegetation change in relation to vegetation degradation or restoration activities.
15 This may however require the regional calibration of WA optima for species and functional
16 groups within regions. In terms of UK plant communities, it appears as though functional
17 group approach may perform slightly better than species in relation to community level
18 fluxes (see supplementary material Fig S1). The limiting factor is that the approach requires
19 the raw species abundance data, which is not always readily available, and a calibration of the
20 NVC communities using co-located flux data, which is also not routinely undertaken. We
21 would therefore encourage researchers to routinely incorporate vegetation measures into
22 studies of methane and other GHG's to allow more comprehensive analyses of the indicator
23 value of vegetation for GHG inventory.

24 The method also has the potential for incorporation into large-scale (national) greenhouse gas

1 accounting programmes (in relation to peatland condition/management). Couwenberg et al.,
2 (2011) have suggested a method for the incorporation of vegetation data into GHG
3 inventories. However, much of their proposed model relies on ‘expert judgement’ and at
4 present we lack sufficient data for a critical evaluation of the use of expert judgement. Of
5 particular concern is the question of scaling up and the transmission of flux and vegetation
6 data from the small scale of chambers (<1m²) to landscapes. We know of no studies where
7 this has been attempted, yet techniques for testing this are available such as eddy covariance
8 and co-located landscape scale vegetation survey.

9 De Deyn et al., (2008) call for a need to identify easily measurable, cost-effective,
10 aboveground traits that capture belowground carbon dynamics across different spatial and
11 temporal scales. Our results strongly suggest that predictive models for methane emissions
12 could be derived using both species (for use in national studies) and/or functional groups (for
13 use in both national and global studies) using abundance data alone. However, we suggest
14 that further study is required using co-located vegetation and methane flux measurements at a
15 range of spatial scales before the links between vegetation and GHG flux are more coherently
16 established.

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4

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1 **Supporting Information**

2 The supporting information includes two tables and one figure comprising the following:

3 Table S1: Attributes used in the classification of functional groups

4 Table S2: Species functional group classification from datasets used in this analysis

5 Figure S1: Predicted CH₄ flux using a weighted average of species and functional group
6 abundance against observed mean CH₄ flux (Log) for National Vegetation Communities for
7 the UK

Peatland methane indicator values

1 Table 1: Details of site characteristics and experimental manipulations and/or management practices. *Modified here means that the vegetation is no
 2 longer indicative of semi-natural bog and has been altered by practices such as drainage, and grazing.

3

Country	Site	Latitude	Longitude	Peatland Type	Altitude (m)	Annual rainfall (mm)	Sub Sites	Experimental treatments/Management practices	total number of plots
Scotland	Auchencorth	55.79 N	3.24 W	*Modified ombrotrophic blanket bog	260	1100	None	9 plots, site drained and sheep grazed	9
							Forsinard	58.37 N	3.97 W
	Sletil	5 semi-natural plots	5						
	Maol Donn	5 semi-natural plots	5						
	Leir	5 semi-natural plots	5						
	Big House	3 burnt and 3 unburnt plots all open to sheep grazing	6						
	Cross Lochs	12 plots of drain blocked, unblocked and 6 semi-natural controls	30						
Whim	55.76 N	3.27 W	280	None	Nitrogen manipulation experiment 4 plots each of NH ₃ , NH ₄ , NO ₃ additions and control	16			
Wales	Migneint	52.99 N	3.80 W	Ombrotrophic blanket bog	480	1100 2000	Migneint A	Blocked and open drains open to (light) sheep grazing	36
							Migneint C	Semi natural open to (light) sheep grazing	8
							Migneint D	Blocked and open drains open to (light) sheep grazing	36
England	Moor House	54.69 N	2.40 W	Ombrotrophic blanket bog	600	1900	Hard Hill	burning 10 year rotation with (light) sheep grazing plots and control plots	16

Peatland methane indicator values

1 Table 2: Results of cross-validation predictions for CH₄ emission from plant species
 2 composition for five sites using weighted averaging from different classification levels,
 3 taxonomic: family, species and dominant species, and functional: functional group and
 4 aerenchymatous/*Sphagnum* spp. only. A 70/30 split was used as training and test sets.

Scale	Classification Level	r ² (adj)	RMSE
Site	Family	0.66	0.18
	Species	0.72	0.14
	Dominant Species	0.67	0.23
	Functional Group	0.81	0.23
	Aerenchymatous/Sphagnum	0.24	0.24
Sub-site	Family	0.44	0.23
	Species	0.52	0.20
	Dominant Species	0.00	0.26
	Functional Group	0.59	0.25
	Aerenchymatous/Sphagnum	0.12	0.26
Treatment	Family	0.13	0.33
	Species	0.25	0.28
	Dominant Species	0.01	0.31
	Functional Group	0.21	0.30
	Aerenchymatous/Sphagnum	0.06	0.31
Plot	Family	0.08	0.34
	Species	0.18	0.30
	Dominant Species	0.14	0.33
	Functional Group	0.23	0.34
	Aerenchymatous/Sphagnum	0.06	0.34

5

1 Figure Legends

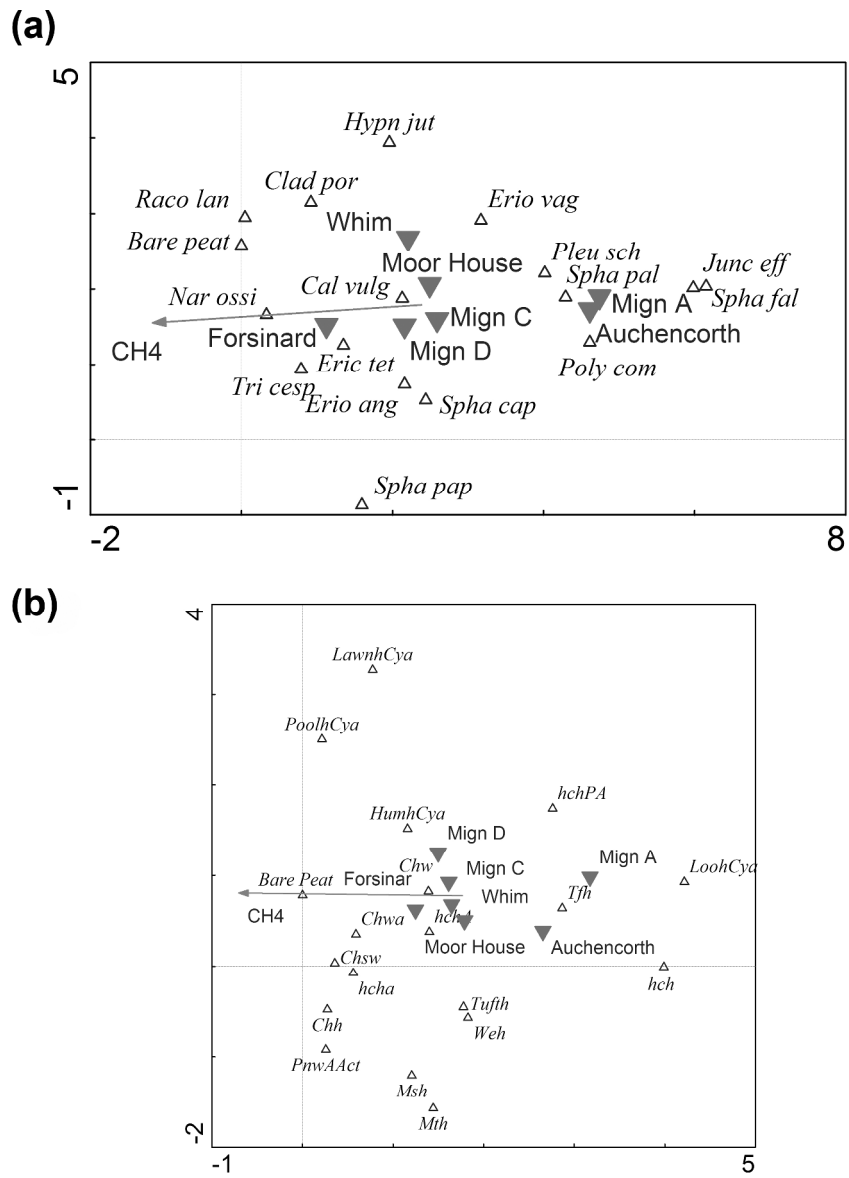
2 Figure 1: DCA biplots of plant species (a) and functional group (b) composition. CH₄
3 flux and site centroids plotted as supplementary variables. Only species with weight
4 above 10% were included for clarity.

5 Figure 2: Methane flux weighted averaged optima and tolerances of plant species and
6 functional group derived from the complete data set.

7 Figure 3: Plots of WA-predicted CH₄ flux (nmol CH₄ m⁻² s⁻¹) using species (a) and
8 functional group (b), versus observed values for the five main sites, sub-sites and
9 treatment plots based on all data. In all plots the black line represents a 1:1 fit. (i) Mean
10 plot level WA predictions for species, $r^2(\text{adj}) = 0.31$, and functional group, $r^2(\text{adj}) =$
11 0.24 . (ii) Mean treatment level WA predictions for species, $r^2(\text{adj}) = 0.39$, and
12 functional group, $r^2(\text{adj}) = 0.33$. (iii) Mean sub-site level WA predictions for species, r^2
13 $(\text{adj}) = 0.59$ and functional group. $r^2(\text{adj}) = 0.80$. (iv) Mean site level WA predictions
14 for species, $r^2(\text{adj}) = 0.91$, and functional group, $r^2(\text{adj}) = 0.96$.

15 Figure 4: Predicted CH₄ flux using a weighted average of functional group abundance
16 against observed median CH₄ flux data from Bubier et al. (1995) and Dias et al. (2010);
17 the UK sites analysed here are also included. The blue line indicates a 1:1 fit ($r^2(\text{adj}) =$
18 0.87). N.B. This Figure has units in mg CH₄ m⁻² d⁻¹ (c.f. Figs 1-3 where units are nmol
19 CH₄ m⁻² s⁻¹) for consistency with the data presented in Bubier *et al.*, (1995) and Dias *et*
20 *al.*, (2010).

Figure 1



289x402mm (300 x 300 DPI)

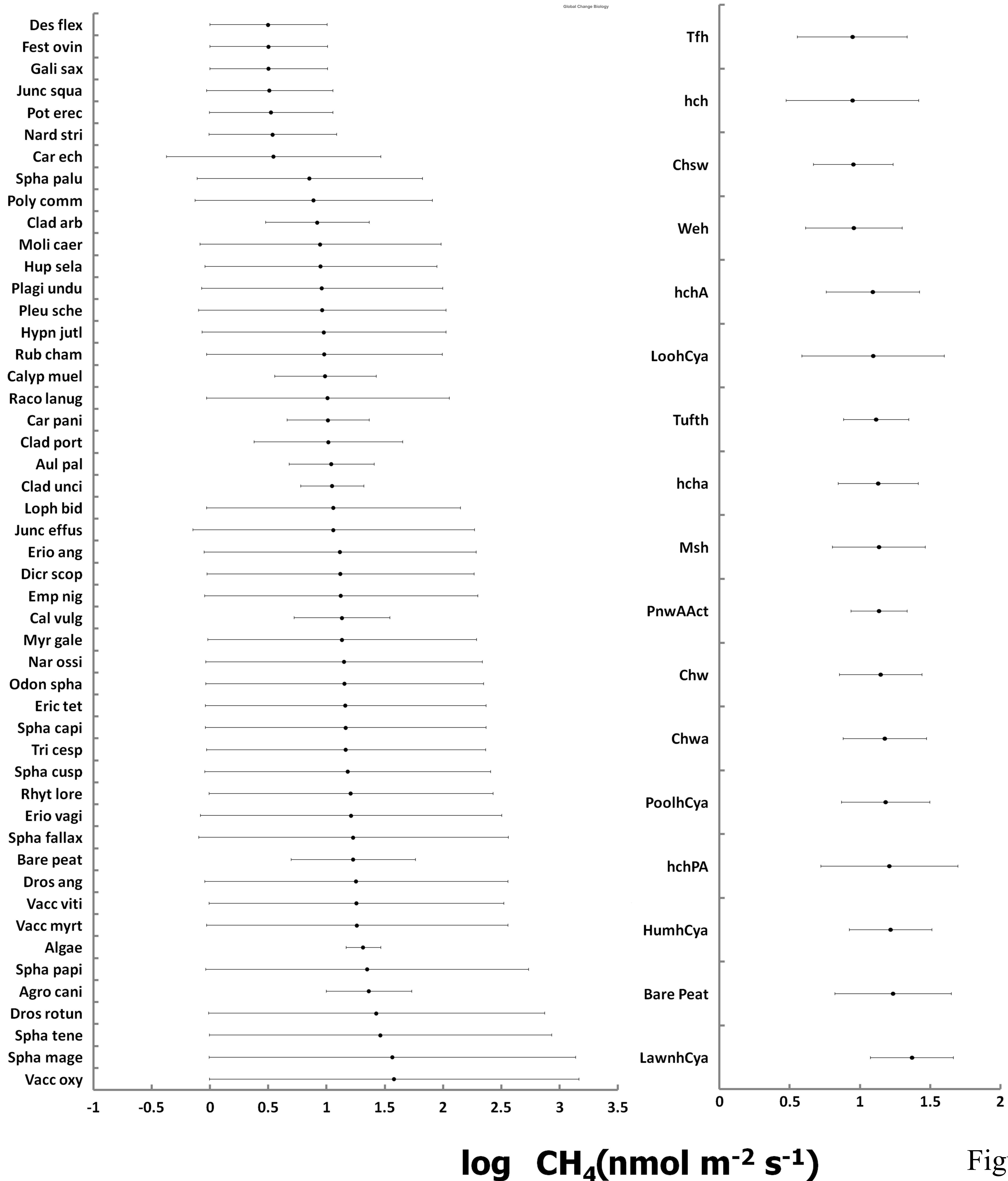


Figure 2

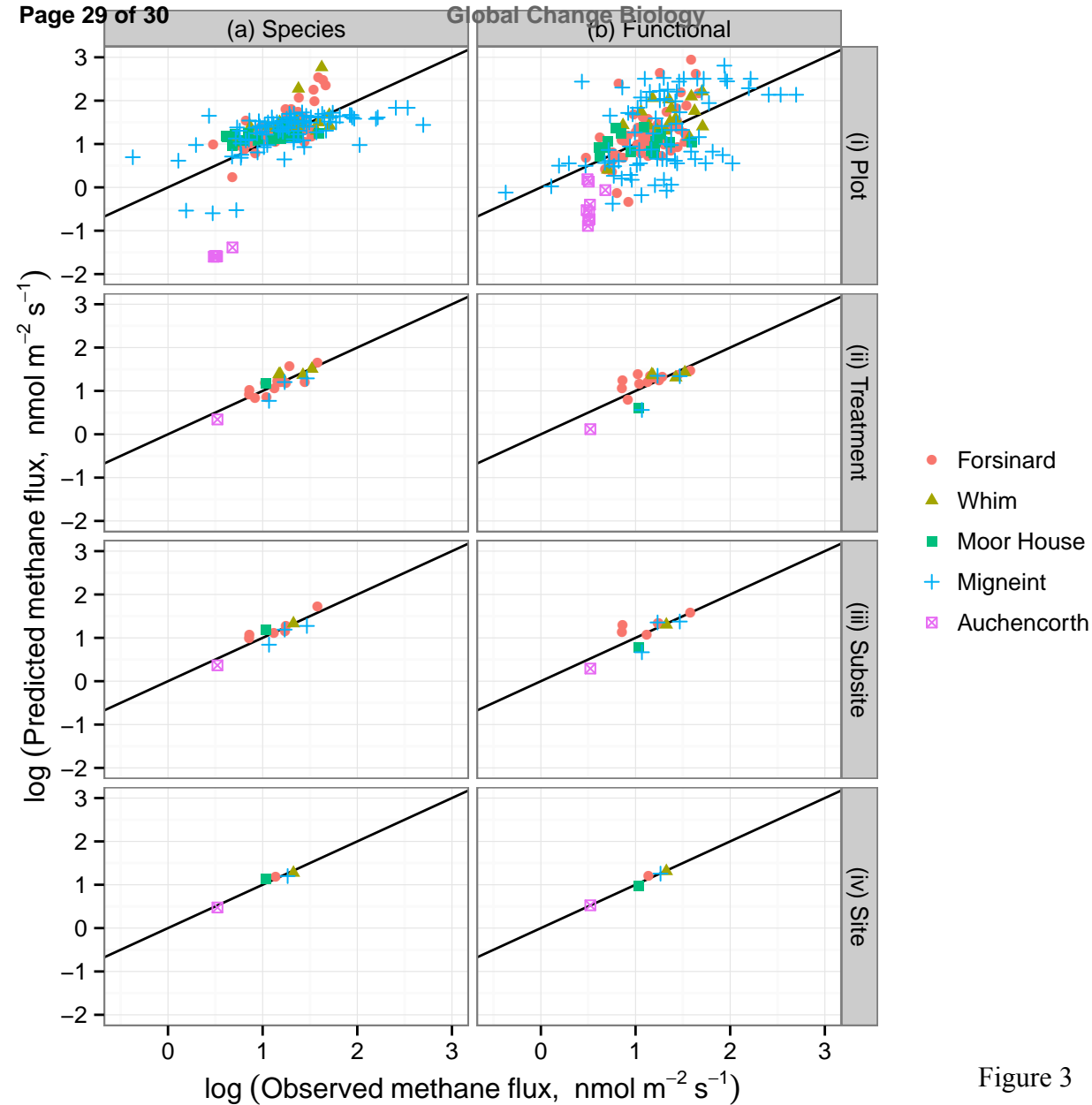
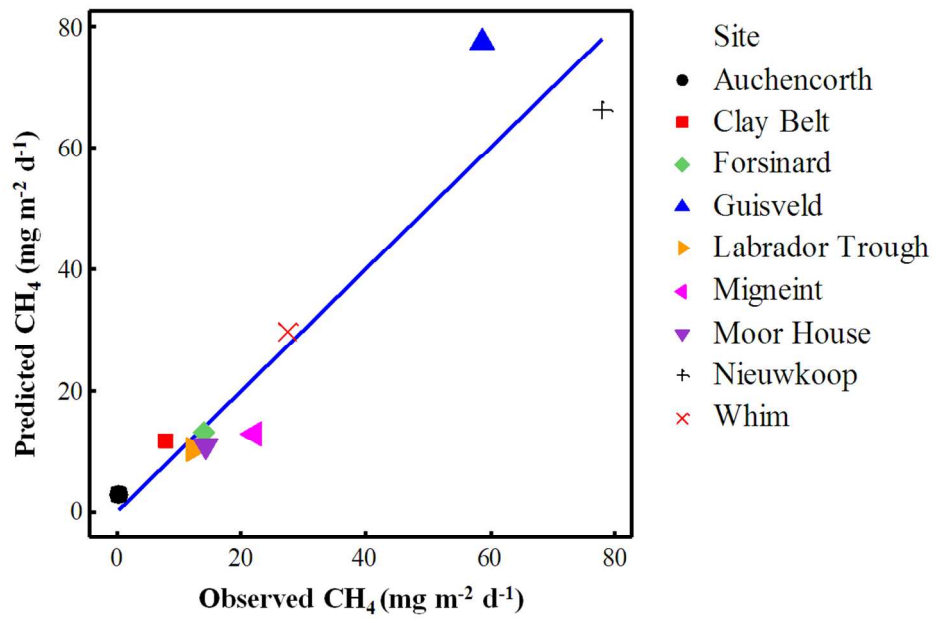


Figure 3

Figure 4



109x73mm (300 x 300 DPI)

Methane Indicator Values for Peatlands: a comparison of taxonomic species and functional groups

Supporting Information

Table S1: Attributes used in the classification of functional groups (from Hill *et al.*, 2007a, Hill *et al.*, 2004). **V** and **NV** superscripts relate to whether traits are associated with vascular or nonvascular plants. Species are attributed to functional groups according to which attributes they possess in relation to life form, woodiness, aerenchyma, N fixation, and an additional standalone type of bare peat. Note that not all life forms shown here were included in our functional groups but they are included for completeness.

Functional trait		
(relationship to CH₄ flux)	Code	Definition
Life Form	Ch	Chamaephyte ^V
(disturbance/decomposition/water table)	Gb	Bulbous geophyte ^V
	Gn	Non-bulbous geophyte (rhizome, corm or tuber) ^V
	hc	Hemicryptophyte ^V
	Hy	Perennial hydrophyte (perennial water plant) ^V
	Hz	Annual hydrophyte (aquatic therophyte) ^V
	Ph	Mega-, meso- and microphanerophyte ^V
	Pn	Nanophanerophyte ^V
	Th	Therophyte (annual land plant) ^V
	Holl	Plants (mainly Sphagnum and other) that are associated with Hollows ^{NV}
	Hum	Plants (mainly Sphagnum and other bryophytes) that are associated with Hummocks
	Lawn	Plants (mainly Sphagnum and other bryophytes) that are associated with Lawns or Mats ^{NV}
	Loo	Plants (mainly Sphagnum and other bryophytes) that are associated with Loose Hummocks ^{NV}
	Pool	Plants found mainly in Pools ^{NV}
	Ac	Aquatic colonial (formless loose colonies) ^{NV}
	At	Aquatic trailing (attached to substrate) ^{NV}
	Cu	Cushion (dome-shaped colonies) ^{NV}
	De	Dendroid (with stolons and erect shoots) ^{NV}
	Fa	Fan (branches in plane on vertical substrate) ^{NV}
	Le	Lemnoid (floating on the water) ^{NV}
	Mr	Mat, rough (creeping, lateral branches erect) ^{NV}
	Ms	Mat, smooth (creeping, branches lying flat) ^{NV}
	Mt	Mat, thalloid (creeping, thalli forming a layer) ^{NV}
	Sc	Solitary creeping (creeping solitary shoots) ^{NV}
St	Solitary thalloid (rosette forming patch not mat) ^{NV}	
Tf	Turf (vertical stems with little or no branching) ^{NV}	
Thread	Thread (solitary thread-like creeping stems) ^{NV}	
Tp	Turf, protonemal (persistent protonema) ^{NV}	
Ts	Turf, scattered (scattered vertical shoots) ^{NV}	
Tuft	Tuft (loose cushions, not dome-shaped) ^{NV}	
We	Weft (intertwining branched layers) ^{NV}	
Woodiness (decomposition substrate)	h	Herbaceous ^{V&NV}
	sw	Semi-woody ^V
	w	Woody ^V
Aerenchymatous (CH ₄ emission)	A	Plants possessing aerenchymatous tissue in the roots ^V
	PA	Plants possessing aerenchymatous tissue and have been shown to have increased methane emission or pressurised flow ^V
	a	Plants assumed to possess aerenchymatous tissue in the roots ^V
N Fixation (CH ₄ emission/root exudation)	Rhi	Rhizobia N fixing ^V
	Act	Actinorhizal N fixing ^V
	Cy	Known relationship with N fixing Cyanobacteria ^{NV}
Bare peat (decomposition)	Bare peat	No above ground vegetation present

Table S2: Species functional group classification from datasets used in this analysis.

Each study is coded as follows: 1-This study; 2 - Bubier et al. (1995); 3 - Dias et al.

(2010). Codes for Figure 1 are shown for this study only.

Plant Type	Species	Author	Functional Groups	Fig 1 code	Study
Vascular	<i>Agrostis canina</i>	L.	hch		1
	<i>Agrostis stolonifera</i>	L.	hch		3
	<i>Alopecurus pratensis</i>	L.	hcha		3
	<i>Anthoxanthum odoratum</i>	L.	hch		3
	<i>Bellis perennis</i>	L.	hch		3
	<i>Calluna vulgaris</i>	(L.) Hull	Chw	Cal vulg	1
	<i>Caltha palustris</i>	L.	hchA		3
	<i>Cardamine pratensis</i>	L.	hcha		3
	<i>Carex acuta</i>	L.	hchPA		3
	<i>Carex cuprina</i>	(I. Sándor ex Heuff.) Nendtv. ex A. Kern.	hchPA		3
	<i>Carex echinata</i>	Murray	hchPA		1
	<i>Carex nigra</i>	L.	hchPA		1
	<i>Carex panicea</i>	L.	hchPA		1+3
	<i>Cerastium fontanum</i>	Baumg.	hch		3
	<i>Cirsium palustre</i>	(L.) Scop.	hcha		3
	<i>Deschampsia flexuosa</i>	(L.) Trin.	hch		1
	<i>Drosera anglica</i>	Huds.	hcha		1
	<i>Drosera rotundifolia</i>	L.	hcha		1+3
	<i>Dryopteris carthusiana</i>	(Vill.) H.P. Fuchs	hchA		3
	<i>Dryopteris cristata</i>	(L.) A. Gray	hchA		3
	<i>Eleocharis palustris</i>	(L.) Roem. & Schult.	hchPA		3
	<i>Empetrum nigrum</i>	L.	Chw		1+3
	<i>Erica tetralix</i>	L.	Chwa	Eric tet	1+3
	<i>Eriophorum angustifolium</i>	Honck.	hchPA	Erio ang	1+3
	<i>Eriophorum vaginatum</i>	L.	hchA	Erio vag	1
	<i>Festuca pratensis</i>	Huds.	hcha		3
	<i>Festuca rubra</i>	L.	hch		3
	<i>Festuca ovina</i>	L.	hch		1
	<i>Galium saxatile</i>	L.	hch		1
	<i>Galium palustre</i>	L.	hcha		3
	<i>Glechoma hederacea</i>	L.	hch		3
	<i>Glyceria fluitans</i>	(L.) R. Br.	hcha		3
	<i>Glyceria maxima</i>	(Hartm.) Holmb.	hcha		3
	<i>Holcus lanatus</i>	L.	hch		3
	<i>Huperzia selago</i>	(L.) Bernh. ex Schrank & Mart.	Chsw		1
	<i>Hydrocotyle vulgaris</i>	L.	hchPA		3
	<i>Juncus acutiflorus</i>	Ehrh.	hchA		3
	<i>Juncus effusus</i>	L.	hchPA	Junc eff	3

Plant Type	Species	Author	Functional Groups	Fig 1 code	Study	
Vascular	<i>Juncus squarrosus</i>	L.	hchA		1	
	<i>Leontodon autumnalis</i>	L.	hch		3	
	<i>Lolium perenne</i>	L.	hch		3	
	<i>Lonicera periclymenum</i>	L.	hch		3	
	<i>Lotus uliginosus</i>	Hoffman	hchA		3	
	<i>Molinia caerulea</i>	(L.) Moench	hchA		1+3	
	<i>Myrica gale</i>	L.	PnwAAct		1	
	<i>Nardus stricta</i>	L.	hch		1	
	<i>Narthecium ossifragum</i>	(L.) Huds.	hcha	Nar ossi	1	
	<i>Pedicularis palustris</i>	L.	hchA		3	
	<i>Persicaria maculosa</i>	Gray	hch		3	
	<i>Phragmites australis</i>	(Cav.) Trin. ex Steud.	hchPA		3	
	<i>Plantago lanceolata</i>	L.	hch		3	
	<i>Poa pratensis</i>	L.	hcha		3	
	<i>Poa trivialis</i>	L.	hcha		3	
	<i>Polygala serpyllifolia</i>	Hose	Chh		1	
	<i>Potentilla anserina</i>	L.	hch		3	
	<i>Potentilla erecta</i>	(L.) Raeusch.	hch		1	
	<i>Ranunculus acris</i>	L.	hch		3	
	<i>Ranunculus repens</i>	L.	hch		3	
	<i>Rhinanthus angustifolius</i>	C.C. Gmel.	hch		3	
	<i>Rubus chamaemorus</i>	L.	hcha		1	
	<i>Rubus sp.</i>	N/A	Pnw		3	
	<i>Rumex acetosa</i>	L.	hch		3	
	<i>Taraxacum officinale</i>	F.H. Wigg.	hch		3	
	<i>Trichophorum cespitosum</i>	(L.) Hartm.	hchA	Tri cesp	1	
	<i>Trifolium repens</i>	L.	hch		3	
	<i>Vaccinium myrtillus</i>	L.	Chw		1	
	<i>Vaccinium oxycoccos</i>	L.	Chwa		1	
	<i>Vaccinium vitis-idaea</i>	L.	Chw		1+3	
	Non Vascular	Algae	N/A	Msh		1
		<i>Aulacomnium palustre</i>	(Hedw.) Schwägr.	Tfh		1+2
<i>Calliergon giganteum</i>		(Schimp.) Kindb.	Tfh		2	
<i>Calliergon stramineum</i>		(Dicks. ex Brid.) Kindb.	Weh		2	
<i>Calypogeia meylanii</i>		H. Buch	Msh		2	
<i>Calypogeia muelleriana</i>		(Schiffner) K. Müller	Msh		1	
<i>Campylium stellatum</i>		(Hedw.) C.E.O. Jensen	Weh		2	
<i>Campylopus atrovirens</i>		De Not.	Tufth		1	
<i>Cephalozia bicuspidata</i>		(L.) Dumort.	Msh		1	
<i>Cephalozia sp.</i>		N/A	Msh		2	
<i>Cinclidium stygium</i>		Sw.	Tfh		2	
<i>Cladonia arbuscula</i>		(Wallr.) Hale & W.L.Culb.	Weh		1	
<i>Cladonia bellidiflora</i>		(Ach.) Schaerer	Tfh		1	
<i>Cladonia chlorophaea</i>		(Flörke ex Sommerf.) Sprengel	Tfh	Clad port	1	

Plant Type	Species	Author	Functional Groups	Fig 1 code	Study
Non Vascular	<i>Cladonia portentosa</i>	(Dufour) Coem.	Weh		1
	<i>Cladonia uncialis</i>	(L.) Weber ex F.H.Wigg.	Weh		1
	<i>Cladopodiella fluitans</i>	(Nees) Jörg.	Weh		2
	<i>Cratoneuron filicinum</i>	(Hedw.) Spruce	Weh		2
	<i>Dicranum polysetum</i>	Sw.	Tufth		2
	<i>Dicranum scoparium</i>	Hedw.	Tufth		1
	<i>Dicranum undulatum</i>	Schrad. ex Brid.	Tufth		2
	<i>Diplophyllum albicans</i>	(L.) Dumort.	Msh		1
	<i>Drepanocladus aduncus</i>	(Hedw.) Warnst.	Weh		2
	<i>Hypnum jutlandicum</i>	Holmen & Warncke	Msh	Hypn jut	1
	<i>Hylocomium splendens</i>	(Hedw.) Schimp.	Msh		1
	<i>Hypogymnia physodes</i>	(L.) Nyl.	Mth		1
	<i>Limprichtia revolvens</i>	(Sw.) Loeske	Weh		2
	<i>Loeskhypnum badium</i>	(Hartm.) Paul	Weh		2
	<i>Lophocolea bidentata</i>	(L.) Dumort.	Weh		1
	<i>Lophozia sp</i>	N/A	Msh		2
	<i>Meesia longiseta</i>	Hedw.	Tfh		2
	<i>Moerckia hibernica</i>	(Hook.) Gottsche	Mth		2
	<i>Mylia anomala</i>	(Hook.) Gray	Msh		2
	<i>Mylia taylorii</i>	(Hook.) Gray	Tufth		1
	<i>Odontoschisma sphagni</i>	(Dicks.) Dumort.	Msh		1
	<i>Oncophorus wahlenbergii</i>	Brid.	Tfh		2
	<i>Paludella squarrosa</i>	(Hedw.) Brid.	Tfh		2
	<i>Plagiomnium ellipticum</i>	(Brid.) T.J. Kop.	Tfh		2
	<i>Plagiothecium undulatum</i>	(Hedw.) Schimp.	Msh		1
	<i>Pleurozium schreberi</i>	(Willd. ex Brid.) Mitt.	Weh	Pleu sch	1+2
	<i>Pohlia nutans</i>	(Hedw.) Lindb.	Tufth		2
	<i>Polytrichum commune</i>	Hedw.	Tfh	Poly com	1+3
	<i>Polytrichum strictum</i>	Menzies ex Brid.	Tfh		2
	<i>Pseudoscleropodium purum</i>	(Hedw.) M. Fleisch.	Weh		1
	<i>Ptilidium ciliare</i>	(L.) Hampe	Weh		1
	<i>Ptilidium pulcherrimum</i>	(Weber) Hampe	Weh		2
	<i>Ptilium crista-castrensis</i>	(Hedw.) De Not.	Weh		2
	<i>Racomitrium lanuginosum</i>	(Hedw.) Brid.	Tfh	Raco lan	1
	<i>Rhytidiadelphus loreus</i>	(Hedw.) Warnst.	Weh		1
	<i>Rhytidiadelphus squarrosus</i>	(Hedw.) Warnst.	Weh		1+3
	<i>Sanionia uncinata</i>	(Hedw.) Loeske	Weh		2
	<i>Scapania sp.</i>	N/A	Weh		2
	<i>Scorpidium scorpioides</i>	(Hedw.) Limpr.	Weh		2
	<i>Sphagnum angustifolium</i>	(Warnst.) C.E.O. Jensen	HumhCya		2
	<i>Sphagnum annulatum</i>	Warnst.	LawnhCya		2
	<i>Sphagnum capillifolium</i>	(Ehrh.) Hedw.	HumhCy	Spha cap	1+2
<i>Sphagnum centrale</i>	C.E.O. Jensen	LoohCya		2	
<i>Sphagnum compactum</i>	Lam. & DC.	LoohCya		2	

Plant Type	Species	Author	Functional Groups	Fig 1 code	Study
Non Vascular	<i>Sphagnum cuspidatum</i>	Ehrh. ex Hoffm.	PoohCy		1
	<i>Sphagnum fallax</i>	H. Klinggr.	LoohCy	Spha fal	1+2+3
	<i>Sphagnum flexuosum</i>	Dozy & Molk.	LoohCya		2
	<i>Sphagnum fuscum</i>	(Schimp.) H. Klinggr.	HumhCya		2
	<i>Sphagnum girgensohnii</i>	Russow	LoohCya		1
	<i>Sphagnum lindbergii</i>	Schimp.	LoohCya		2
	<i>Sphagnum magellanicum</i>	Brid.	LawnhCy		1+2
	<i>Sphagnum majus</i>	(Russow) C.E.O. Jensen	LoohCya		2
	<i>Sphagnum palustre</i>	L.	LoohCya	Spha pal	3
	<i>Sphagnum papillosum</i>	Lindb.	LawnhCy	Spha pap	1
	<i>Sphagnum platyphyllum</i>	(Lindb.) Warnst.	LoohCya		2
	<i>Sphagnum pulchrum</i>	(Lindb.) Warnst.	LoohCya		2
	<i>Sphagnum russowii</i>	Warnst.	HumhCya		2
	<i>Sphagnum subnitens</i>	Russow & Warnst.	HumhCya		2
	<i>Sphagnum tenellum</i>	(Brid.) Brid.	LoohCy		1
	<i>Sphagnum tenerum</i>	Sull. & Lesq. ex Sull.	HumhCya		2
	<i>Sphagnum warnstorffii</i>	Roll	LoohCya		2
	<i>Tomenthypnum falcifolium</i>	Ren. ex Nich.	Tfh		2
	<i>Tomenthypnum nitens</i>	(Hedw.) Loeske	Tfh		2
<i>Warnstorfia exannulata</i>	(Schimp.) Loeske	Weh		2	
N/A	Bare Peat	N/A	Bare Peat	Bare peat	1

Figure S1: Predicted CH₄ flux using a weighted average of species and functional group abundance against observed mean CH₄ flux (Log) for National Vegetation Communities for the UK. Plots were classified according to the NVC community they best fitted by a weighted species match and then an NVC community mean for observed and WA flux estimates were calculated. The blue line indicates a 1:1 fit (species r^2 (adj) - 0.46; functional group r^2 (adj) - 0.85). Bare peat is a not an NVC community but indicates those plots where bare peat dominates and NVC community was ambiguous. NVC communities are: M1 - *Sphagnum auriculatum* bog pools; M2 - *Sphagnum cuspidatum/recurvum* bog pools; M6 - *Carex echinata*, *Sphagnum auriculatum/recurvum* mire; M15 - *Scirpus cespitosus*, *Erica tetralix* wet heath; M16 - *Erica tetralix*, *Sphagnum compactum* wet heath; M17 - *Scirpus cespitosus*, *Eriophorum vaginatum* mire; M18 - *Erica tetralix*, *Sphagnum papillosum* mire.

