Approaches to Bayesian occupancy modelling for habitat quality assessment
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Summary

- Bayesian 'occupancy' models (BOM) are a powerful tool that have recently been adapted to deal with 'opportunistic' species data (i.e. biological records).
- Individual species trends from any models can be aggregated to produce habitat indicators; here this is demonstrated for BOMs and Frescalo (Hill, 2012) using two examples.
- Example one demonstrates the production of habitat-specific trends using NPMS indicator species and subsets of 1 x 1 km grid cells predicted to contain the habitat of interest from Land Cover Mapping. Decisions around whether to include subsets of habitat-containing cells, or all cells within a political boundary, will be important for trend interpretation: habitat subsets of cells may lead to biases depending on true habitat change over time.
- Example two compares BOMs to the Frescalo method, as well as investigating the impacts of decisions for indicator production (e.g. weighting or not weighting by a species national frequency) on the trends produced. In this example weighted trends for 18 *Sphagnum* species typical of blanket bog were much more similar than unweighted trends.
- In the case of contradictory habitat (or species) trends it will not normally be possible to know which model is correct (at least in the absence of an unbiased dataset to which to refer). Given that BOMs, as currently used, may contain significant bias, a prudent approach would be to compare the outputs of several methods before making decisions.

Introduction

Hierarchical Bayesian modelling (HBM) is an important technique in the modern ecologist's toolbox (Hilborn & Mangel 1997; McCarthy 2007; Kéry & Royle 2016). HBM provides the opportunity to specify complex models that are unavailable using more standard statistical interfaces, and is considered by some to be transforming the practice of ecology (Gimenez *et al.* 2014; Hooten & Hobbs 2015). Bayesian occupancy models (BOM), a particular type of HBM developed within ecology, are one example of this trend. BOM were developed in order to account for the typically imperfect detectability of species during surveys (Royle & Dorazio 2008); in their simplest form they separate the human process of detection from the ecological quantity of interest, the presence or absence of a species for example. This statistical separation can be crucial for the accurate discovery of ecological pattern; for example, Marc Kéry and colleagues (2010a; 2010, 2011) have repeatedly drawn attention to the biases that imperfect detection can potentially bring to the elucidation of ecological relationships.

Bayesian occupancy modelling as currently applied to 'opportunistic' biological records data involves several additional assumptions and modifications to standard occupancy models (Kéry *et al.* 2010a,b, van Strien *et al.* 2010, 2013). In addition to the assumption of fixed detectability during a survey (or 'closure') period, models of opportunistic data use survey-level information to help account for variation in detectability estimates. To date, the most successful of these Bayesian approaches (as assessed against simulated data) has been an extended detectability model which includes 'list length' (i.e. the number of taxa observed on a given day visit to a grid cell) as a surrogate for recorder effort (Isaac *et al.* 2014). Non-Bayesian methods have also been used to

account for certain types of bias in biological records; for example the method of Hill (2012) is based on the premise that, at large scales (e.g. large clusters of 10 x 10 km grid cells), relative frequency curves across species show common patterns, and that the frequency of the commonest *n* species within this curve will provide information on survey effort with which to adjust the relative frequencies of other species.

Within what follows, it is important to keep in mind that analyses of unstructured (or semi-structured; Pescott *et al.* 2015) data that attempt to adjust for the various kinds of biases contained within biological records (Powney & Isaac 2015) will inevitably make assumptions about the structure of the data modelled; whether or not a model captures the actual structure of the data well will be a key determinant of its success. The use of multiple models may therefore be useful in corroborating conclusions—if common conclusions are reached using different models, then we may be more confident that any particular conclusion is reliable. Note, however, that if models result in contradictory conclusions, it will not normally be possible to tell conclusively which model is at fault (at least in the absence of a 'gold standard' of high quality, unbiased data). As is elaborated below, it may also be the case that patterns elucidated at different scales conflict—this can be the case even in the absence of bias (Wiens 1989).

In the current report we explore the potential for BOM to be used to model trends in species that are characteristic of certain habitats, with the aim of producing habitat quality indicators. In general, habitat 'quality' cannot be defined without reference to some standard of high quality against which habitat patches are to be assessed (JNCC 2004). In this paper, however, we report on the potential for BOM to produce trends based on lists of species representative of particular habitats; this approach, or similar, could be applied to lists of species endorsed by habitat experts as being appropriate for the aim of indicating the quality of national stocks of any particular habitat. We do not investigate the issue of the most appropriate list of species for any particular habitat here. We do note the existence of species indicators of habitat quality within the Common Standards Monitoring approach to condition assessment for Sites of Special Scientific Interest (SSSIs; JNCC 2004), the lists of habitat indicators used by the new National Plant Monitoring Scheme (Walker *et al.* 2015), and the lists of 'axiophytes' or 'worthy plants' developed by the Botanical Society for Britain and Ireland (BSBI) (see http://bsbi.org/axiophytes; in addition, an axiophyte dataset compiled by Dr K.J. Walker, Head of Science, BSBI, will be available soon at http://eidc.ceh.ac.uk). Other potential indicator lists may be available, and can be easily be incorporated using the framework outlined below.

Within this report we demonstrate two approaches to creating habitat quality metrics using Bayesian Occupancy Models. For one of these cases we also compare the BOM trends to those produced by a separate, modelling process with different assumptions (Frescalo; Hill 2012).

Example 1: Vascular plants in habitat-specific grid cells

Introduction
In this example we focus on species associated with certain habitat types by using the habitat indicators as defined by the National Plant Monitoring Scheme (NPMS; http://www.npms.org.uk); indicator species within habitats for this scheme were originally chosen by randomly sampling those species that were abundant and/or frequent in the synoptic tables of associated UK National Vegetation Classification habitats (Rodwell 1991 et seq.), followed by expert review. Species were also filtered on their national (i.e. British) frequency at the 2 x 2 km scale, and the ease with which they can typically be identified by naturalists (based on verification rules originally produced by expert botanists for the National Biodiversity Network). Here we focus on NPMS habitat types that can be linked to existing land-cover maps (Appendix 2). The aim is to produce a separate indicator for each habitat type. Lowland heathland and broadleaved woodland are the candidate habitat types used to explore the potential of this approach here.

The example examined here is an indicator of habitat quality in the sense that trends in species typical of a particular habitat are likely to reflect a trend in habitat quality at the scale of the data (assuming that 'quality' is defined as having some relation to the identity of the species present in a habitat). For example, we assume that a decline in woodland quality would result in a decline in the occupancy (i.e. the frequency of occurrence in 1 x 1 km grid cells) of woodland species in woodland habitats. This approach is distinct from monitoring activity conducted at finer scales (e.g. quadrats in woodlands, where data would typically be collected at 10 x 10 m or similar depending on the focal vegetation stratum). The proposed approach to a BOM-based indicator therefore embodies a trade-off: a large body of data, collected in a relatively unstructured manner by both professional and amateur botanists, at a relatively large scale (1 x 1 km), is used to draw inferences concerning the occupancy of species at that scale. We expand on the validity of the assumptions embodied by this approach in the discussion section below.

Methods
Data
Occurrence records of vascular plants within 1 x 1 km grid cells in the UK were extracted from the BSBI Distribution Database (http://bsbidb.org.uk). The time-period used for the indicators was 1987 to 2013, as this represents a core period of recording for these taxa in the UK (Preston *et al.* 2002). In this example, we use only those grid cells that contain what is expected to be a significant proportion of the given habitat type, based on recent remote-sensing data (Morton *et al.* 2011). Woodland grid cells were selected as those cells containing greater than 50% coverage of broadleaved woodland (*n* = 1722), while the selection criteria for lowland heathland cells chose those with greater than 25% coverage of heather and heather grassland combined, and which were less than 300 m in mean altitude (*n* = 14076) (see Appendix 2 for further details on the selection and definition of these habitats). These subsets were chosen as they retained a considerable proportion of the target-habitat containing 1 km grid cells, whilst also ensuring that trends in associated species are likely to be from the habitat of interest (rather than other habitats contained within a selected grid cell). The spatial distribution of the 1 x 1 km grid cells (hereafter called 'monads') included in the analysis for each habitat type is shown in Figure 1. It may be that, given the highly fragmented state of heathland in lowland England, a lower percentage cover threshold is required for heathland monads, currently there appears to be an under-representation of lowland heath in this area (cf. for example the map in Lake *et al.* 2014).
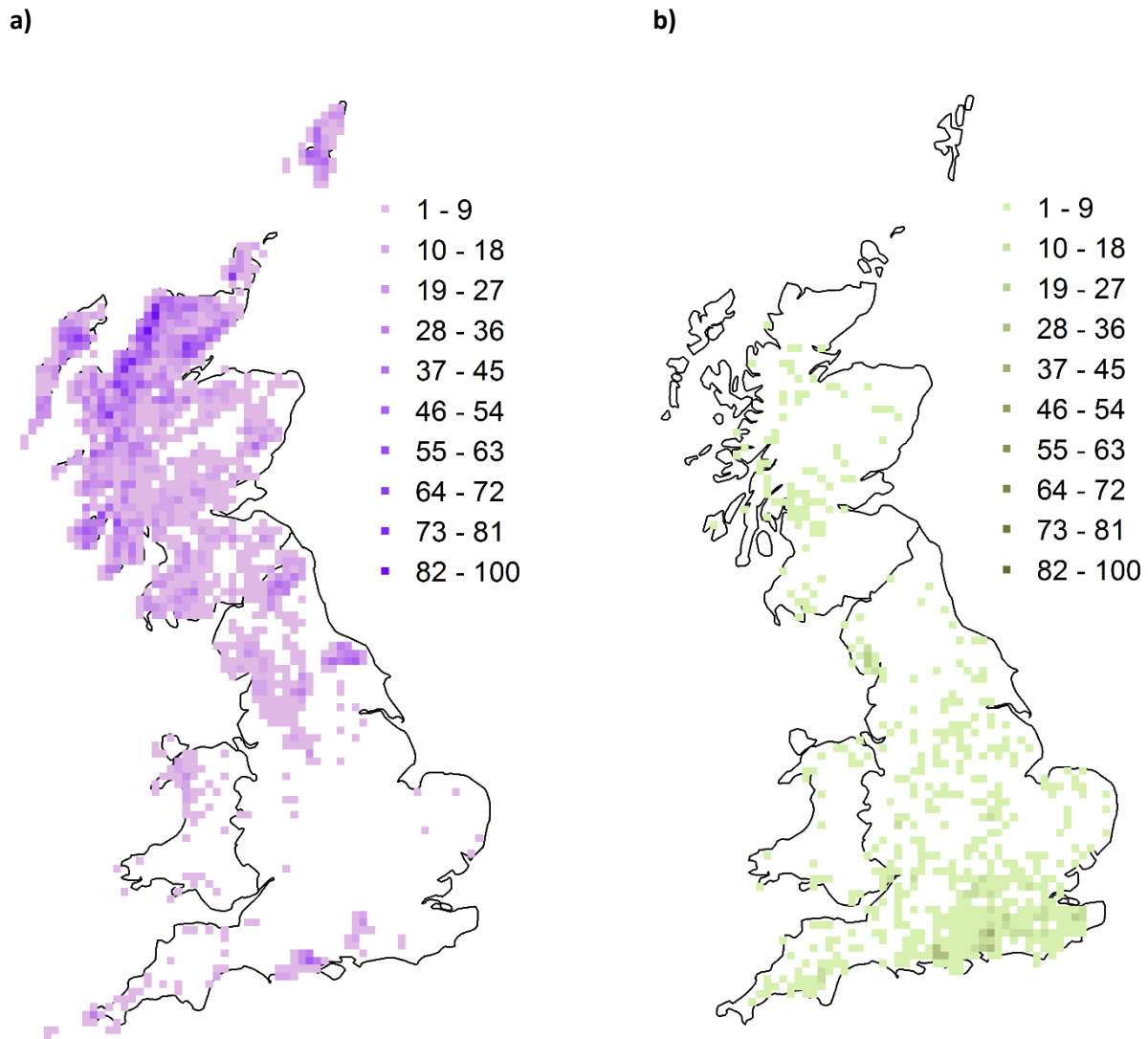
a)   b)

Figure 1. The distribution and density of monads from which the trend estimates were derived for the two habitat indicators: a) lowland heath; and, b) broadleaved woodland. The shading represents the number of unique monads within each 10 x 10 km grid cell included in the analysis (10 x 10 km cells are used for visualisation reasons only).

Analysis

We ran BOMs for two sets of approximately 30 species, one for each habitat type (see Appendix 1 for the full species lists). These species were derived from the NPMS list of species indicative of dry heathland and deciduous woodland (Appendix 2). We used the Bayesian indicator workflow described in the development of the UK Biodiversity Indicators Technical Background Document (Isaac *et al.* 2015) to produce the indicators and generate species-specific credible interval trends for each habitat type. The procedure of Isaac *et al.* (2015) calculates growth rates on the log odds scale, and uses the posterior distribution (i.e. uncertainty) of these rates to calculate confidence intervals; see the discussion section of Example 2 below for more discussion on the choice of method for summarising across species.

Results

The lowland heath and deciduous woodland indicators are based on 23 and 21 species respectively (Appendix 1 - note that several species failed the inclusion criteria). Not all species contribute to all years (see *No. spp.* column in Table 1) due to the species:year inclusion criteria laid out in Isaac *et al.*

(2015). Both indicators tended to be stable across the entire study period of 1987 to 2013 (Figure 2). More specifically, the smoothed trend for woodland shows a steady increase in occupancy until 2005, after which the trend levels off. Both indicators have relatively wide credible intervals, with a maximum width of approximately 150 (where the index = 100% in year 1), representing high uncertainty in our annual index estimates. The proportion of species showing long-term increases and decreases were roughly equal for both habitat types (see Figures 3a-d below), a result which was reflected in the stable indicator plots. In contrast, over the short-term, a larger proportion of heathland species were increasing than declining (Figure 3b), while the reverse was true for the woodland species (Figure 3d, i.e. a greater proportion have suffered declines than increases).
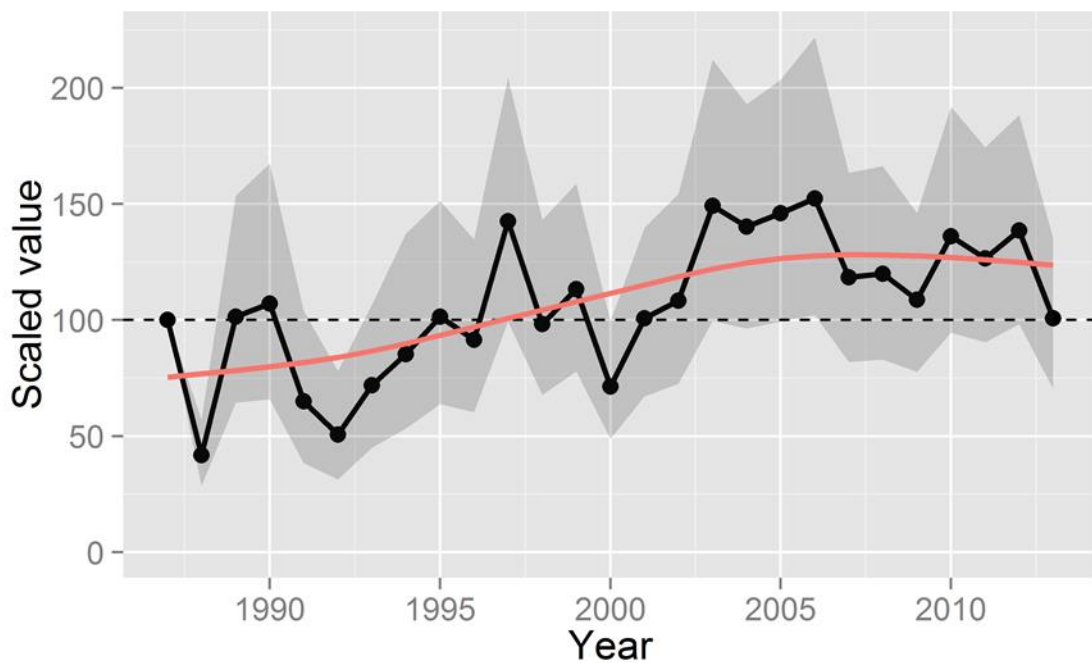
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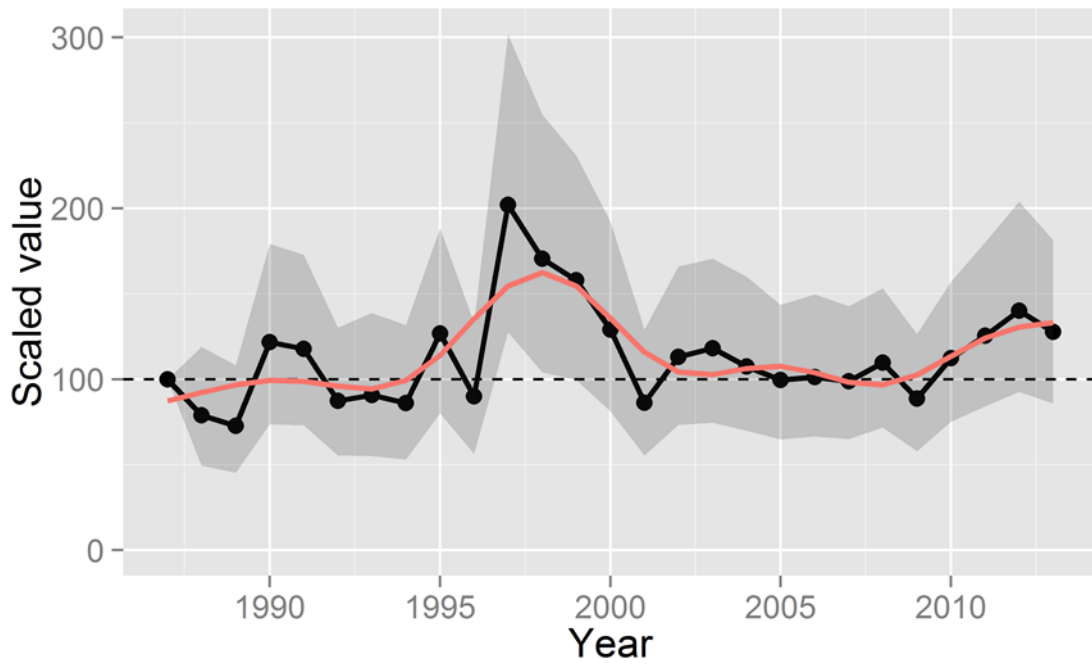
b)

Figure 2. Change in the log-odds of occupancy between 1987 and 2013 for a) heathland and b) woodland indicator species. The shaded region represents the 90% credible intervals for the annual index estimates. The red line illustrates a smoothed trend estimated from a GAM fitted to the rescaled indicator values.)
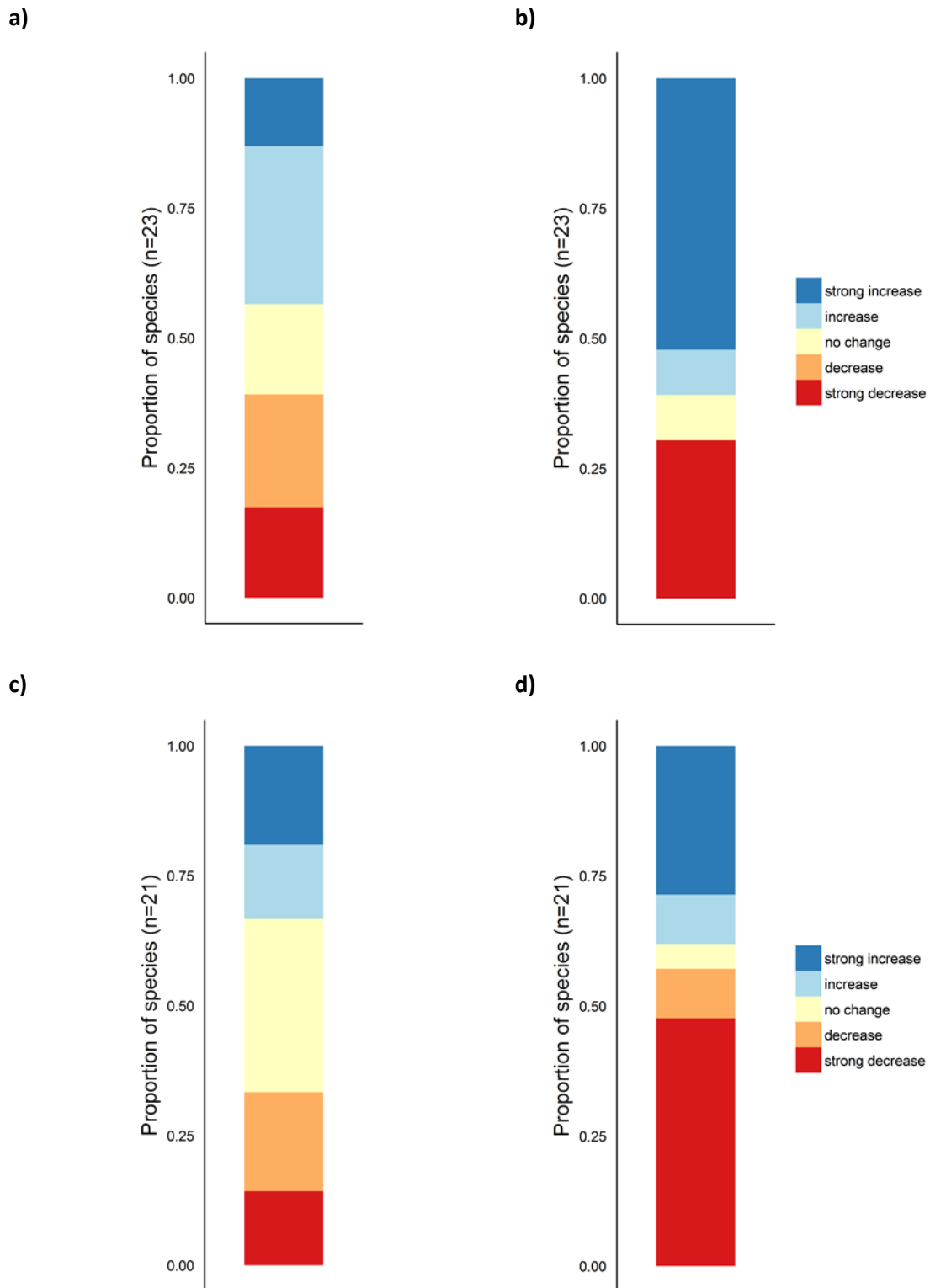
a)

b)

c)

d)

Figure 3. The proportion of dry heath (a, b) and deciduous woodland (c, d) indicator species in each trend category based on mean change in occupancy over both a, c) the long-term (all years) and b, d) the short term (the most recent five years).

Table 1. Change in occupancy between 1987 and 2013 for a) lowland heathland and b) woodland indicator species. The indicator values per year are presented alongside their uncertainty (upper and lower 90% CI), and the number of species contributing to the annual index value. The number of species contributing has been split into those with an interpolated estimate and those with an actual occupancy estimate.

a)

Year	Indicator	Lower CI	Upper CI	Smoothed indicator	No. spp. estimated	No. spp. interpolated
1987	100	100	100	87.26	22	0
1988	78.97	49.34	118.85	92.23	21	1
1989	72.68	45.28	108.26	96.65	20	2
1990	121.63	73.68	179.08	99.26	22	1
1991	117.69	73.01	172.74	98.79	22	1
1992	87.38	55.34	130.09	95.88	23	0
1993	90.65	54.94	138.77	94.26	21	2
1994	86.03	53.02	131.73	99.30	21	2
1995	126.86	80.02	188.28	113.98	22	1
1996	89.96	56.27	132.76	135.33	21	2
1997	202.04	127.58	301.80	154.63	23	0
1998	170.56	104.10	254.82	162.35	21	2
1999	158.00	99.56	230.91	154.48	21	2
2000	128.97	81.17	192.08	135.59	20	3
2001	86.17	55.47	129.09	115.87	22	1
2002	113.06	73.31	166.03	104.26	23	0
2003	118.12	74.63	170.56	102.75	22	1
2004	107.34	69.80	159.96	106.22	23	0
2005	99.59	64.84	143.41	107.59	23	0
2006	101.31	66.52	149.75	103.88	23	0
2007	98.77	64.96	142.81	98.26	21	2
2008	109.76	71.78	153.18	96.72	22	1
2009	88.58	57.86	126.32	102.53	23	0
2010	112.22	75.18	157.06	113.49	22	1
2011	125.39	84.13	180.07	124.11	23	0
2012	140.02	92.64	203.98	130.49	23	0
2013	127.65	85.83	181.43	133.24	23	0

b)

Year	Indicator	Lower CI	Upper CI	Smoothed indicator	No. spp. estimated	No. spp. interpolated
1987	100	100	100	75.36	21	0
1988	41.76	30.32	54.96	76.81	21	0
1989	101.49	69.40	141.31	78.30	15	6
1990	107.03	70.20	152.43	79.89	14	7
1991	64.98	41.65	94.59	81.73	14	7
1992	50.71	33.39	73.37	83.96	12	9
1993	71.87	47.81	101.32	86.67	19	2
1994	85.35	57.12	123.64	89.84	20	1
1995	101.49	68.26	144.01	93.37	19	2
1996	91.52	65.03	127.01	97.07	20	1
1997	142.60	104.10	190.20	100.76	21	0
1998	98.32	71.05	132.76	104.38	21	0
1999	113.31	81.91	148.00	107.95	21	0
2000	71.42	52.17	93.49	111.53	21	0
2001	100.69	72.68	134.44	115.16	21	0
2002	108.27	76.79	146.06	118.72	20	1
2003	149.16	105.79	201.29	121.97	21	0
2004	140.23	104.87	182.68	124.65	21	0
2005	146.00	105.60	189.31	126.58	21	0
2006	152.30	110.14	205.38	127.70	21	0
2007	118.46	87.42	155.51	128.14	21	0
2008	119.93	88.89	155.13	128.07	21	0
2009	108.72	81.18	139.67	127.63	21	0
2010	136.01	100.72	180.06	126.92	21	0
2011	126.54	94.84	162.95	125.96	21	0
2012	138.60	102.53	179.83	124.82	20	1
2013	100.76	75.14	128.46	123.59	21	0

Discussion

The indicators presented here focus on subsets of 1 x 1 km cells where the habitats of interest are estimated to be at high cover. However, grid cells meeting a particular criterion of habitat cover may change over time (woodland may be planted or grubbed-out; heathland may be destroyed or restored etc.). Trends are presented here between 1987 and 2013, but the selection of grid cells for modelling uses habitat cover values estimated around 2007 (i.e. the use of the CEH 2007 Land Cover Map). This means that cells that had already experienced severe habitat degradation or destruction by 2007 are not likely to be included in the indicator. This may bias the trend in the indicator upwards. Conversely, habitat newly created or restored post-2007 are also absent from the 2007-2013 component of the trend, biasing the indicator downwards. It is not possible to know which of these biases, if either, dominates the trends graphed here.

One way of coping with these potential, but very hard to quantify, biases would be to randomly select monads for inclusion in the indicator (or to simply include all British or UK monads for every subset of species), however, both these approaches would also increase the variance in the indicator, and could potentially introduce more noise from the occurrence of some of the species in the indicator lists outside of target habitats (e.g. many 'look-a-like', non-native infraspecific taxa are planted in gardens and escape into peripheral habitats, particularly for the woodland indicator species; Sell 2006). An alternative strategy for coping with the potential biases caused by habitat grid cell choices would be to combine land cover information from a wider selection of datasets; for example, all three CEH Land Cover Maps (1990, 2000, 2007) could be combined, with any cell having >*X*% of land cover *Y* included. This would help to cope with temporal biases in grid cell selection, although it should also be remembered that remote sensing technology and classification approaches will have changed between maps, and therefore for some land cover types, particularly those subject to high classification error, such union sets over time may still contain inappropriate grid cells. Given that our approach selects the majority of the British stock of a particular habitat by selecting 1 x 1 km cells from the 2007 CEH Land Cover Map, we expect that, at least in the short to medium term, these locations will be the most suitable for monitoring changes in habitat quality (as judged by occupancy trends of indicator species).

The estimated trends, even with the statistical adjustments introduced by the Bayesian occupancy modelling approach, are likely to still contain bias; furthermore, patterns of 1 x 1 km cell occupancy are unlikely to match dynamics at the plot scale, particularly for widespread species. For example, national evidence for declines in the light-loving element of the woodland ground flora of Britain (Kirby *et al.* 2005) may not be reflected in trends at a larger scale, for the simple reason that botanists collecting data for distribution-focused projects will generally cover more ground whilst surveying, meaning that a larger variety of habitats are searched. Species that may have declined inside of woodlands (e.g. where coppicing or other management has ceased), may survive on woodland rides or edges, or where localised disturbance has opened canopy gaps. It should therefore be noted that trends established at different scales may not be congruous: this does not mean that one trend is incorrect and another correct, it is merely an instance of differing scale-dependent patterns. For this reason, ecological and other contextual knowledge should always be brought to bear on the interpretation of indicators.

Changes in habitat 'quality', defined as the presence or absence of indicator species, could be attributable to increases or decreases in area of habitat within a 1 x 1 km cell, if a standard species-area relationship tends to hold in habitat fragments in the UK. In addition, plant indicators of high-quality habitat (Kimberley *et al.* 2013) tend to be slow at dispersing to new habitats, due to particular trait combinations (e.g. large seeds, vegetative spread), therefore over the time periods relevant to this indicator we expect that the loss of species at the 1 x 1 km cell level will indicate habitat loss (or a degradation in quality, which we take to be equivalent), while increases are likely

to be either from restoration efforts (whether reintroductions or management that restores suitable conditions for a species present in a seed bank), or from marginal gains at the edges of 1 x 1 km cells. Increases could of course also be attributable to under-recording in the past, although the Bayesian occupancy model was used to partially address this issue where enough data exist within a year to estimate detectability. Another related issue that will need addressing in future versions of indicators of this type is the exclusion of data relating to non-native infraspecific taxa nested within the species used as indicators: e.g. the inclusion of records of *Lamiastrum galeobdolon* ssp. *argentatum* within the trend estimated for *L. galeobdolon* (Yellow Archangel) is likely to be responsible for the increase in occupancy: this non-native subspecies is generally considered to be increasing in urban and sub-urban woodlands, and may also be increasingly better recorded by botanists due to gradual changes in the recording culture resulting in greater attention being paid to garden escapes and other non-natives.

Example 2: Bryophytes at the national level

Introduction
In this example national biological records data for bryophytes (Blockeel *et al.* 2014) are used to investigate the congruence between BOM and the Frescalo method (Hill 2012). The choice of bryophytes is dictated by the recent availability of a large and spatially extensive quality-assured dataset (Blockeel *et al.* 2014); this dataset has also been analysed in detail using Frescalo, a methodology designed to cope with variable recording intensity (Hill & Preston 2014), but not so far subject to BOM (with the exception of 7 'priority' bryophyte species included in the JNCC 2015 Priority species indicator C4b; http://jncc.defra.gov.uk/page-6850).

In this example we use data in our BOMs at a marginally coarser scale than for vascular plants, the 2 x 2 km grid cell (hereafter referred to as a 'tetrad'). This is due to the fact that considerable amounts of bryophyte data are collected at this resolution, particularly in recent years (Preston & Rorke 2014). Note that bryophyte surveyors may still make records at finer resolutions, but that this will frequently be in the context of sampling a tetrad (Preston *et al.* 2012). Using a finer scale for BOM, such as the 1 × 1 km grid cell, may mean that the covariable 'list length' does not truly represent the effort expended during a recording session; for example, a recorder may record all the species that they can find in a single monad and then visit the other three monads in a tetrad only briefly in order to add additional species. In this case species yielded by visits into neighbouring monads may be associated with short lists at the monad level (although this of course depends on local beta diversity at the scale of the vegetation community, and on the effort expended by the surveyor in these monads).

The Frescalo trends presented here are calculated using the same dataset as the BOM models, for the same 5-year time periods; however, the trends are produced at the 10 x 10 km (hectad) scale. Although trends can be scale-dependent (Keil *et al.* 2011), the recent use of Frescalo at the hectad scale in a national atlas (Hill & Preston 2014) makes it desirable to compare these two approaches at the scale at which they are likely to be applied. Note that the use of longer time periods, and coarser spatial grain, must increase the number of replicated site visits within a closure period: this should result in better estimates of detectability (Kéry & Royle, 2016).

Finally, this example also examines the use of weights in the production of trends (van Strien *et al.* 2012).

Methods
Data
Data were extracted from the database of the British Bryological Society (held at the Biological Records Centre, CEH Wallingford; also see https://data.nbn.org.uk/Datasets/GA000144). Data were summarised to tetrad or hectad presences for 5-year periods as detailed above; the periods used were: 1985-89; 1990-94; 1995-1999; 2000-04; 2005-09; and 2010-2013. Annual indices were not produced due to the fact that bryophyte recorders are unlikely to revisit the same grid cell within a single year; using 5-year closure periods is more likely to result in meaningful detectability (and occupancy) estimates due to an increased opportunity for repeat visits (under the assumption that species occupancy is relatively stable within a 5-year window). For some groups of taxa species aggregates were used; this ensures that changes in taxonomic focus across the time period modelled does not produce false trends (Jansen & Dengler 2010; Hill & Preston 2014, 2015).

In the example presented here, 18 *Sphagnum* species given a frequency class score of 3 ("[a] normal habitat or substrate for the species") for blanket bog (EUNIS class D1) in the bryophyte attributes database 'BRYOATT' were used (Hill *et al.* 2007). These species are listed in Table 2 below.

Table 2. *Sphagnum* species and species aggregates for which blanket bog (EUNIS class D1) is a normal habitat. For aggregate definitions see Hill *et al.* (2007).

Sphagnum balticum	*Sphagnum majus*
Sphagnum capillifolium	*Sphagnum molle*
Sphagnum cuspidatum	*Sphagnum palustre*
Sphagnum denticulatum s.l.	*Sphagnum papillosum*
Sphagnum fuscum	*Sphagnum pulchrum*
Sphagnum girgensohnii	*Sphagnum recurvum s.l.*
Sphagnum imbricatum s.l.	*Sphagnum riparium*
Sphagnum lindbergii	*Sphagnum strictum*
Sphagnum magellanicum	*Sphagnum tenellum*

Due to the issues discussed above in Example 1, and also due to the desire to produce results comparable with the analyses of Hill & Preston (2014), grid cells were not restricted to habitat subsets in this example: all grid cells, at the resolution modelled, sampled during the period 1985-2013 were used.

Analysis

We used the Bayesian occupancy model described in the development of the UK Biodiversity Indicators Technical Background Document (Isaac *et al.* 2015) to produce the indicators and generate species-specific trends for each habitat type, with the exception that the logistic regression for detectability was specified as:

$$\text{logit}(p_{ivt}) = a_t + \beta_1.LL_{vt} + \beta_2.Date_{vt} + \beta_3.Date^2_{vt} + \varepsilon_v$$

Where p_{ivt} is the probability of species i being detected on visit v within time period t; a_t is a (5 year) time period-specific random effect; LL_{vt} is the list length from visit v within time period t; $Date_{vt}$ and $Date^2_{vt}$ are the Julian date of visit v within time period t and its second order polynomial; and ε_v is a random error term. That is, we posit that detectability is influenced by the time of year and by recorder effort.

Frescalo analyses followed the approach outlined in Hill & Preston (2014).

Indicator production followed standard advice for the taking of the geometric mean (geomean) across individual species' trends (van Strien *et al.* 2012). Either the median of the posterior distribution (BOM) or the Frescalo relative frequency measure for the time period 1985-90 was taken as the starting point for the indicators; subsequent measures were re-scaled relative to this initial value. For the purpose of this test, measures of uncertainty around these point estimates from both model types were ignored, as has often been the case in indicator production (Gregory *et al.* 2005). The implications of this are discussed below.

For weighted geomeans, the weights were specified as:

$$w_i \ = \ N_i / N_{max}$$

Where, the species weight w_i is calculated as the number of hectads in which a species was recorded during 1985-2013 (N_i), divided by the number of hectads occupied during this period by the most widespread species considered in the indicator (N_{max}), here *Sphagnum palustre*. Van Strien *et al.* (2012) provide the formula for the calculation of weighted geomeans.

Results

The different approaches produce quite different indicators, as can clearly be seen in Figure 4 below. The discrepancy between approaches is greater for the unweighted than the weighted geomean. The two modelling approaches (BOM, Frescalo) give quite different pictures of change using the unweighted geomean, whereas with weighted geomeans they are likely to be indistinguishable, particularly if one considers the uncertainty associated with individual species' trends (typically assessing using bootstrapping, but not presented here).
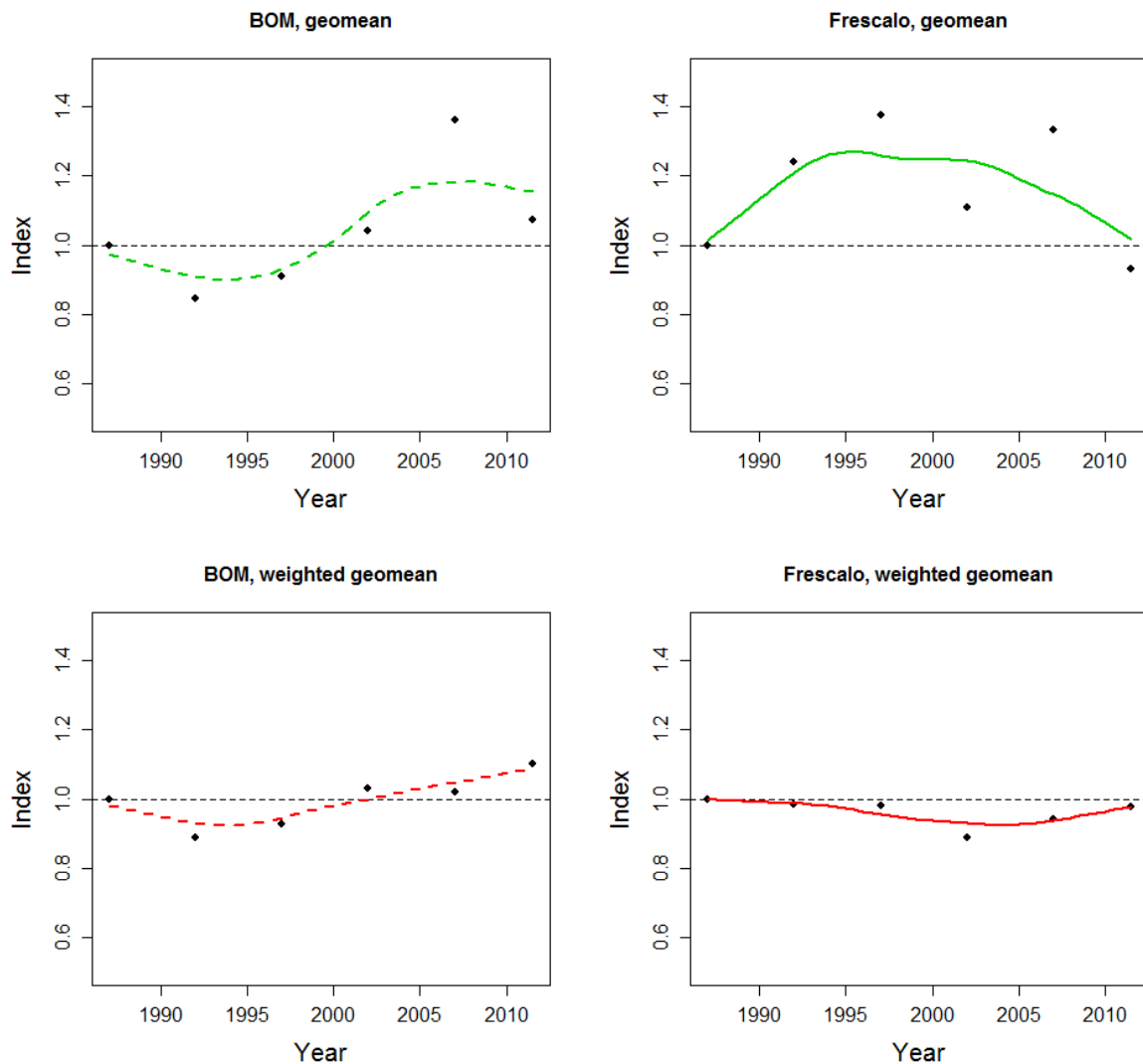

Figure 4. Experimental indicators for *Sphagnum* species associated with blanket bog; produced either using Bayesian Occupancy Models (BOM) or Frescalo (Hill, 2012), and with and without species weights. Trend lines

are Gaussian family local polynomial regression ('loess') fits calculated in *R* using the loess.smooth function with default settings (span = 0.75, degree = 2).

Discussion

The development of appropriate biodiversity indicators is not trivial, and there is no shortage of discussion in the literature concerning approaches (e.g. Buckland *et al.* 2005; Gregory *et al.* 2005; Nielsen *et al.* 2007; Lamb *et al.* 2009; van Strien *et al.* 2012). The approach used in this example is a standard one based on the geomean (van Strien *et al.* 2012).

The increased variability in the indicator trends produced using the geomean is not unexpected, given that the practice of rescaling species abundance or occupancy values to the first year of a time series can produce large index values in some years for rare species, because these species may show large relative change even for small distributional increases. This effect of the geomean is in general desirable, and has been one of the reasons for its selection when producing trends from abundance data: relative changes are often considered to be more biologically relevant, and can be related to population growth rates (Isaac *et al.* 2015). However, it also means that rare species exert the same influence as commoner ones; this may be less desirable for indicators produced using opportunistic data, because rare species may be more likely to violate model assumptions, or to lack data. A weighted geomean may help with this issue (van Strien *et al.* 2012), and means that, whilst relative change in the distributions of rare species is taken into account, change for the commonest species dominates the index. This may be desirable if the 'condition' (*sensu* Common Standards Monitoring) of widespread habitats is under consideration; for other purposes, monitoring improvements in populations of rare species may be a key focus for an indicator. The simple weighting used here means that common species, particularly if the method is applied across large areas, will dominate the index; note however, that many other weighting schemes are possible, for example, the relative index of occupancy used here could be logged, producing a much less variable set of weights.

Finally, note that the example presented here is considerably simpler than that used in example 1 (described in Isaac *et al.* 2015), but that the Bayesian approach used there to construct confidence intervals is just as applicable to the geometric mean as it is to the change in log odds approach. The choice between the change in log odds approach and the geometric mean approach deserves further consideration. Due to the non-linear shape of the logit curve, approaches using the change in the log odds of occupancy between time periods mean that species occupying intermediate proportions of the area modelled will exert less influence on the indicator than both the rarer and the commoner species. This is because a greater change in occupancy is required around 0.5 to produce a given change in the log odds, relative to occupancies closer to 0 and 1; for example, a change from 0.5 to 0.6 on the log odds scale is 0.41, whereas the change from 0.01 to 0.1 is 2.41. This may be desirable for some applications, but the impacts of this decision on indicator production deserves to be further explored, particularly in combination with the influences of species' weights.

Conclusions

The recent past has seen a considerable expansion in the approaches available for indicator development. This report has attempted to review and demonstrate some of the possibilities and challenges of these methods. Whilst Bayesian occupancy modelling is now considered to be a reliable method for constructing trends from 'opportunistic' biological records data (Kéry *et al.* 2010a; Isaac *et al.* 2014), a greater understanding of the implications of unmet model assumptions would strengthen the claim of the approach to be the 'gold standard'. For example, if little real information on detectability exists in a dataset (i.e. if the detectability logistic regression explains little of the variation in the data), then the variance in occupancy probabilities may be considerable. In addition, both Royle (2006) and Kéry & Royle (2016) point out that "unmodelled site-specific heterogeneity in detection will lead to underestimates of occupancy" (Kéry & Royle, 2016, pp. 560-561). Likewise, if the relationship between detectability and its covariables is biased in some way (e.g. rare species are often recorded in short lists), then occupancy probabilities will also be biased. Kéry & Royle (2016, p. 559) provide the following example: "if multiple surveys [i.e. replicates within a temporal closure period] are only undertaken at the "better" sites, where density and therefore detection probability (p) may be higher on average, the resulting estimate of p will be biased high with respect to all sites and therefore the occupancy estimator will be biased low". A similar logic pertains to the example where rare species are disproportionately recorded on short lists: for example, if the information in observation data suggests that there is a negative relationship between list length and a species being observed (because it has been the target of special, focused, surveys), then detectability will be biased upwards for short lists, biasing the occupancy estimator downwards, despite that fact that, all else being equal, a 'random search' model of recording implies that rare species should have low detectability.

In addition to these issues of model reliability, greater discussion around the appropriateness of different approaches to indicator construction would be beneficial (cf. van Strien *et al.* 2012); different approaches emphasise different aspects of the underlying species trends, and an approach that is fit for purpose in one situation may be less appropriate in a second. Comparisons between approaches are also likely to be useful, particularly if independent experts are recruited to 'sense-check' both species' and aggregated trends.

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Appendix 1. The list of species included in the two habitat indicators. * = Species that failed the inclusion criteria, therefore do not contribute to the indicator. The Change Index (Telfer *et al.*, 2002) for each species from the *New Atlas* (Preston *et al.*, 2002) is included for reference. Additionally, species were grouped into one of five categories based on their long-term trend in occupancy, strongly negative (--), negative (-), no change (NC), positive (+), strongly positive (++). Note that the *New Atlas Change Indices* were calculated across all British 10 x 10 km cells, rather than a set of habitat-specific 1 x 1 km cells.

Woodland species	*New Atlas* Trend	Long-term trend	Lowland heath species	*New Atlas* trend	Long-term trend
Allium ursinum	0.24	+	Calluna vulgaris	-0.64	-
Campanula latifolia*			Cerastium fontanum	1.40	+
Campanula trachelium	0.14	--	Cuscuta epithymum*		
Carex sylvatica	0.05	+	Dactylorhiza maculata	-0.42	NC
Ceratocapnos claviculata	0.57	NC	Deschampsia flexuosa	-0.22	+
Corylus avellana	-0.54	-	Digitalis purpurea	0.72	++
Cynoglossum officinale*			Empetrum nigrum	-0.29	+
Daphne laureola	0.10	++	Erica cinerea	-0.94	+
Euphorbia amygdaloides	-0.22	NC	Galium saxatile	-0.15	+
Galium odoratum	-0.62	NC	Genista anglica	-1.09	--
Geum urbanum	-0.53	++	Hypochaeris radicata	0.61	++
Ilex aquifolium	-0.16	++	Jasione montana*		
Lamiastrum galeobdolon	1.07	NC	Linum catharticum	-0.44	--
Neottia ovata	-0.54	NC	Lotus corniculatus	1.09	NC
Melica uniflora	-0.04	-	Nardus stricta	-0.68	-
Mercurialis perennis	-0.65	NC	Pedicularis sylvatica	-1.28	NC
Milium effusum	0.31	-	Plantago coronopus	0.16	NC
Moehringia trinervia*			Platanthera bifolia	-1.67	--
Mycelis muralis*			Polygala serpyllifolia	-0.50	--
Ruscus aculeatus	0.74	++	Polygala vulgaris*		
Sanicula europaea	-0.98	--	Sedum anglicum	-0.21	-
Silene dioica	-0.44	+	Serratula tinctoria	-0.21	+
Teucrium scorodonia	-0.69	NC	Stachys officinalis*		
Veronica montana	0.48	-	Thymus pulegioides*		
Viola riviniana	1.07	--	Thymus polytrichus	-0.64	-
Viola reichenbachiana*			Ulex minor	0.20	++
			Ulex gallii	0.20	-
			Vaccinium myrtillus	-0.61	+

Appendix 2.

a. Broadleaved woodland
NPMS guidance definition
(http://www.npms.org.uk/sites/www.npms.org.uk/files/PDF/NPMS%20Guidance%2
0Notes_WEB_0.pdf):
"Dry deciduous woodland: includes natural or semi-natural woodlands with
canopies made up of one or more of the following native broad-leaved deciduous
species: Birch, Beech, Ash, Aspen, Pedunculate/Sessile Oak, Rowan, Large/Small-
leaved Lime, and Wych Elm."

NVC definition used to create Indicator level species list within the NPMS (expert-
reviewed):

NVC code	NPMS habitat	Weight[*]
W10	Dry deciduous woodland	1
W11	Dry deciduous woodland	1
W12	Dry deciduous woodland	1
W13	Dry deciduous woodland	1
W14	Dry deciduous woodland	1
W15	Dry deciduous woodland	1
W16	Dry deciduous woodland	1
W17	Dry deciduous woodland	1
W8	Dry deciduous woodland	1
W9	Dry deciduous woodland	1

*A weight of 1 indicates that the constituent NVC community is not split between NPMS habitats. Here,
all the NVC constituent communities only contribute to the NPMS habitat 'Dry deciduous woodland'.

b. Lowland heathland
NPMS guidance definition
(http://www.npms.org.uk/sites/www.npms.org.uk/files/PDF/NPMS%20Guidance%2
0Notes_WEB_0.pdf):
"Dry heathland: occurs on dry, sandy soil and is dominated by Heather and Bell
Heather, usually with Common or Western Gorse. Typically dry heathland occurs in
the lowlands often near to the coast, in south west, south east and eastern England
and Wales (Gower, Pembrokeshire and Anglesey) as well as on sand dunes in
Scotland. It is also found in a mosaic of coastal habitats in Northern Ireland (e.g.
Galboly, Co. Antrim) and alongside lowland blanket bog habitats (e.g. Slieve Beagh.
Co. Fermanagh). Dry heathland can extend into milder and wetter upland regions of
northern England and Scotland where it is more commonly called 'moorland' or
'grouse moor'. As well as Heather and other dwarf-shrubs, characteristic species
include Heath Bedstraw, Tormentil and Heath Milkwort."

NVC definition used to create Indicator level species list within the NPMS (expert-
reviewed):

NVC code	NPMS habitat	Weight[*]

H1	Dry heathland	1
H11	Dry heathland	1
H2	Dry heathland	1
H3	Dry heathland	1
H4	Dry heathland	0.5
H5	Dry heathland	1
H6	Dry heathland	1
H7	Dry heathland	0.5
H8	Dry heathland	0.5

* Here, some of the NVC constituent communities also contributed to the definition of other NPMS habitat categories (e.g. H4, H7 and H8).

Link habitat types to CEH Land Cover Map.

a. The NPMS 'Dry deciduous woodland' category may simply be linked across to the CEH Land Cover Map 2007 'Broadleaved woodland' category in the first instance. Note that the Land Cover Map Broadleaved woodland category includes much woodland planted for amenity or forestry; the selection of 1 x 1 km cells could be further restricted through the use of the Natural England Ancient Woodland Inventory.

b. The NPMS habitat 'Dry heathland' is more challenging to match to the CEH Land Cover Map 2007. The NPMS habitat definition includes three NVC communities that can also contribute to other NPMS categories, as shown below (NVC communities that occur within other NPMS habitats highlighted):

NVC code	NPMS habitat	Weight
H1	Dry heathland	1
H11	Dry heathland	1
H2	Dry heathland	1
H3	Dry heathland	1
H4	Upland heathland	0.5
H4	Dry heathland	0.5
H5	Dry heathland	1
H6	Dry heathland	1
H7	Dry heathland	0.5
H7	Maritime cliffs and slopes	0.5
H8	Dry heathland	0.5
H8	Upland heathland	0.5

This is inevitable, given the existence of gradual transitions between, or mosaics within, habitat types in the real world. However, the CEH Land Cover Map category 'Heather' contains the following sub-categories, Heather & dwarf shrub; Burnt heather; Gorse; Dry heath; in addition to 'Heather', 'Heather grassland' contains areas of lower density heather that are likely to be areas of degraded heathland. 'Heather' and 'Heather grassland' were separated from wet heath and bog by the use of a peat depth variable during the production of the LCM (see http://www.ceh.ac.uk/documents/lcm2007datasetdocumentation.pdf). Montane habitats are also separated out by altitude in the LCM, hence, the equivalence of the NPMS category 'Dry heathland' and the CEH LCM categories 'Heather' + 'Heather grassland' should be a reasonable approximation.

Given the above, the 1 x 1 km cells that have a high coverage of the LCM categories 'Broadleaved woodland' and 'Heather' + 'Heather grassland' should, respectively, be appropriate locations for monitoring the biodiversity of these habitats at a relatively large scale.