Article (refereed) - postprint

Smart, S.M.; Jarvis, S.; Walker, K.J.; Henrys, P.A.; Pescott**, O.L.**; Marrs, R.H.. 2015. **Common plants as indicators of habitat suitability for rare plants; quantifying the strength of the association between threatened plants and their neighbours**. *New Journal of Botany*, 5 (2). 72-88. 10.1179/2042349715Y.0000000011

Common plants as indicators of habitat suitability for rare plants; quantifying the strength of the association between threatened plants and their neighbours

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Abstract

Rare plants are vulnerable to environmental change but easy to over-look during survey. Methods are therefore needed that can provide early warnings of population change and identify potentially suitable vegetation that could support new or previously overlooked populations. We developed an indicator species approach based on quantifying the association between rare plants across their British ecological range and their suite of more common neighbours. We combined quadrat data, targeted on six example species selected from the Botanical Society of Britain and Ireland's Threatened Plant Project (TPP), with representative survey data from across Britain. Bayes Theorem was then used to calculate the probability that the rare species would occur given the presence of an associated species that occurred at least once with the rare species in the TPP quadrats. These values can be interpreted as indicators of habitat conditions rather than expectations of species presence. Probability values for each neighbour species are calculated separately and are therefore unaffected by biased recording of other species. The method can still be applied if only a subset of species are recorded, for example where weaker botanists record a pre-selected subset of more easily identifiable neighbour species. Disadvantages are that the method is constrained by the

availability of quadrats currently targeted on rare species and results are influenced by any recording biases associated with existing quadrat data.

Keywords: biodiversity, Bayes theorem, habitat assessment, global change, conservation

Introduction

Regional species pools are typically characterised by a small number of widespread species and a larger number of rare species (Magurran & Henderson 2003) and the vascular plant flora of Britain is no exception (Rabinowitz *et al.,* 1981). Addressing the conservation of each rare species proportionately and effectively is therefore a major challenge. Britain has the luxury of comparatively excellent data on the occurrence of its rare species, especially plants, but records are often resolved at the grid square (10 x 10km to 100x100m), and not at the habitat-patch scale. While these data support a large number of studies of distributional change and relationships to driving variables (e.g. Henrys *et al.,*2011; Powney *et al.,*2014) more detailed habitat patch-scale information is needed to understand the dependence of rare species on particular configurations of abiotic conditions and therefore to highlight potential threats linked to drivers of change in these conditions (Aikens & Roach 2014; Wamelink *et al.,* 2014; Marcer *et al.,* 2013; Huston 1999). A number of approaches to this problem are possible but all are ultimately data constrained (Lomba *et al.,* 2010). Detailed studies of the population dynamics of a plant species can be used to parameterise models of population turnover including dispersal between patches of suitable habitat (Sletvold *et al.,* 2013; Bucharova *et al.,* 2012). However, such studies are costly and the resulting models may often lack the ability to predict how population growth rates respond to interacting global change drivers (Crone *et al.,* 2011). A simpler approach, and therefore applicable to more species, is to attempt to characterise the realised niche by jointly recording abiotic data and occupancy from patches across a species' geographic range, preferably including unoccupied patches beyond the range margin so as to ensure that climatic constraints can also be identified (Henrys *et al.,* in press; Wamelink *et al.,* 2003; Rowe *et al.,* 2015). This method depends on adequate coverage of a species' realised niche, which is often not feasible because of the scarcity of fine-scale data that sample the entirety of each rare species' biogeographic range (Gogol-Prokurat 2011). Niche models can be constructed based on very few recorded presences but the resulting niche description is quite likely to be ecologically incomplete. Moreover it may only be possible to build models if the few presences are coupled with a much larger number of absences. This can result in spuriously impressive model performance unless models are evaluated against independent test data (Lobo *et al.,* 2008; Bahn & McGill 2013; Randin & Dirnbock 2006).

We present an example of an approach based on identifying the more frequent associates that tend to grow alongside the rare plant. These faithful neighbours can then be used to infer the suitability of habitat conditions for the rarer species without necessarily measuring these associated conditions. The method is easily repeated and the indicator list updated as more quadrats are recorded that sample more of the rare species' range. This method also circumvents the need to make arbitrary decisions about the number and ecological range of absence data assumed to represent unfavourable niche space (Fig 1). Thus we define a list of neighbours as any species that grows alongside the rare species. Absence data is then defined as all locations where any one of the neighbour species has been recorded but in the absence of the rare species (Fig. 1). Our reasoning is as follows: Consider a rare species that is obligately dependent on another more common species but not the other way around; if the rare species is present then the more common species must be present. However, if the rare species is not recorded then the reliability of the common species as an indicator of appropriate conditions for the rarity is lessened the more that the common species grows under a wider range of conditions than those associated with the rarity. We recognise that it is not just abiotic factors that are responsible for influencing rare plant population size. Variation in demography (Freckleton & Watkinson 2002; Yenni *et al.,* 2012), reproductive biology (Pocock *et al.,* 2006; Kunin & Gaston 1997), phylogeography and dispersal (Pigott & Walters 1954; Kimberley *et al.,* in press) and negative and positive interactions with other species including mycoheterotrophy (Jarvis et al 2015; Selosse *et al.,* 2006) can explain why some species are restricted in their geographic range, habitat specificity and local population size (Rabinowitz et al 1981). We proceed on the assumption that particular configurations of abiotic conditions are at least a critical pre-requisite for rare species persistence (e.g. Wamelink *et al.,* 2014) and that identifying faithful neighbours is a useful tool to help rapidly compare potentially suitable vegetation patches. In recognition of the fact that additional factors may be required to more fully explain a particular species' abundance we emphasise that the faithfulness of neighbour species is interpreted as indicating varying habitat suitability rather than varying probability of presence.

This faithful neighbour approach seeks to identify indicator species on a continuum where the best indicator always grows with the rare species, and never elsewhere. However, such an optimal indicator would also, by definition, be as rare as the rare species of interest in the habitats sampled although it could still be more detectable because its populations were always larger. At the other extreme, a plant species may always have been recorded accompanying the rare species, but if it occurs very widely elsewhere its presence is not likely to be a good discriminator of suitable conditions for the rare species. For any rare species, we would expect to identify a range of possible indicators that vary in the strength of their association with a rare species. The approach lends itself to the following applications:

1. Early-warning monitoring of a possible reduction in the suitability of conditions for extant rare plant populations by reference to changes in the presence of neighbouring plant species.
2. Initial assessment of the suitability of sites for re-introduction of the rare species.
3. Locating new or pre-existing populations based on identifying floristically appropriate vegetation patches in a wider area of search.

Deriving indicator species in this way depends on data availability; datasets are needed that sample the rare species and its neighbours and that represent the wider geographic range and habitat affinities of the neighbours in situations where the rare species is not found. Here, we used extensive GB-wide survey datasets covering the majority of common and rare vegetation types. These data have already been used to develop Species Niche Models for a large proportion of British vascular plants and bryophytes (De Vries *et al.,* 2010; Henrys *et al*. in press). Coverage of rare species was based on species-compositional data from the Threatened Plant Project (TPP) organised by the Botanical Society of Britain and Ireland (BSBI).

The TPP was a five-year survey to assess the status of 50 of Britain and Ireland's most threatened plants using a standardised and repeatable methodology. Species were chosen from a broad spectrum of ecological conditions but with a bias towards infertile, semi-natural habitats in the lowlands. Species also differed in terms of their distributional range, but were similar in having suffered recent declines. Data were collected to provide an assessment of recent trends, including drivers of change, and to quantify the ecological and management requirements of these rare and threatened species. The aim was to aid targeting of conservation management, refine national 'threat' status and provide a baseline from which future population changes could be assessed. For each species a sample of populations was drawn at random from high-resolution records collected since 1970. The sample was stratified by vice-county (subdivisions of land area used to organize recording of the flora of the UK) with number of locations proportional to the number of records per vice-county. These locations were revisited between 2008 and 2012. Plant species growing with the threatened focal plant were also identified by recording the species composition of 2m diameter circular quadrats co-located with the rare species population. These data were used in combination with the GB-wide survey data to quantify the extent to which other more common plant species tended to grow with the rare species, and therefore to identify possible indicators of suitable habitat for the rare species. The strength of the association was quantified by the probability that the rare species will be present given the presence of the more common associate. This probability was calculated for every plant species recorded growing with each of the TPP rare species. Here we present the results of this analysis for six of the TPP species namely *Astragalus danicus, Blysmus compressus, Gentianella campestris Oenanthe fistulosa, Polystichum lonchitis* and *Vicia orobus*. These species were chosen to represent a range of habitats across Britain and because their ecological requirements were well known to the authors such that the results could be readily assessed for their plausibility. Nomenclature follows Stace (2010) for vascular plants and Hill *et al.,* (2008) for bryophytes.

Methods

Study species

Astraglaus danicus is a low-growing perennial of dry, infertile grassland where competition from other species is low. It grows best at low altitudes in short calcareous grassland in the eastern and south-eastern England. In northern England, Scotland and the Isle of Man it occurs in grassland associated with base-rich rock outcrops, cliff-tops and sand dunes. Populations on the Aran Islands in Western Ireland occur on deposits over limestone pavement. It appears to have declined substantially in southern and northern England, largely due to agricultural improvement or lack of grazing. Less is known about populations in Scotland and Ireland which are presumably stable.

Blysmus compressus is a rhizomatous perennial of open mire, marsh and fen vegetation, dune slacks and in damp grassland, often by flushes, springs and riversides. The species is widespread but localised across England, rare in Scotland and Wales and not recorded from Ireland. It has been assessed as Vulnerable in Great Britain due to substantial declines attributed to changes to hydrology, loss of habitat, nutrient enrichment and reduced grazing levels.

Gentianella campestris is a short biennial that grows in mildly acid to neutral, low fertility soils, and is most often found in open, grazed, species-rich pastures, maritime heath, dune slacks and machair where competition from other species is low. It is widespread but localised throughout Scotland, north Wales, north and west Ireland and northern England, but is very rare in England south of the Pennines. Substantial losses are recorded from across its range over the last 50 years, leading to an assessment of Vulnerable in GB and Endangered in England and Wales.

Oenanthe fistulosa is an umbellifer of damp, seasonally inundated weakly acid to weakly basic soils. Plants persist in lightly shaded conditions but are weak competitors. Ideal conditions for *O. fistulosa* comprise areas of bare damp soil for germination and a grazing or cutting regime to create open areas and restrict the growth of more vigorous wetland species. Widespread but declining across much of southern England, Ireland and coastal regions of Wales, it is a rare species in Scotland and is assessed as Vulnerable in GB.

Polystichum lonchitis is a montane fern confined to rock outcrops, screes and limestone pavements in upland regions of England, Wales, Scotland and Ireland. It is a very slow growing species that is susceptible to grazing, burning, and collecting. British and Irish populations are at the southern edge of its range and therefore may also suffer as a result of climate change.

Vicia orobus is a tall, perennial member of the pea family found on sloping, free-draining neutral to mildly-acid soils across a range of habitats, including low fertility pastures and hay meadows, mires, stream banks, ravines, sea cliffs, limestone heath and woodland margins. The bulk of the GB population is found in Wales. Elsewhere, it is thinly scattered throughout the southern uplands and along the west and north coast of Scotland, and is rare in Ireland and England. *Vicia orobus* is assessed as Near Threatened in GB and Vulnerable in England, but is of Least Concern In Wales.

Datasets

TPP quadrat data was provided by the BSBI (Table 1a). In addition, datasets were required covering British vegetation as a whole, and from which quadrat data could be extracted representing the ecological range of each of the neighbour species recorded at least once with each of the six species in the TPP quadrat data (Table 1b). Quadrats from both datasets were combined to form one subset of data per TPP species for analysis. In the TPP subset every quadrat contained the rare species while the contextual data was defined by the fact that every plot contained at least one of the neighbour species found growing at least once with the TPP species in the TPP dataset.

Quantifying the association of rare species with their neighbours

We combined the contextual GB data and the TPP data to define the probability (P) that a rare (r) species will be present given the presence of a neighbour (n) species as follows;

$$P(r|n) = \frac{P(n|r) * P(r)}{(P(n|r) * P(r)) + (P(n|r') * P(r'))}$$

This is a simple application of Bayes Theorem (Webb & Westover 1997). The data required for this equation are as follows:

$n \cap r$	the number of plots containing the rare species and the neighbour,
$n \cap r'$	the number of plots containing the neighbour but not the rare species,
$r \cap n'$	the number of plots containing the rare species but not the neighbour.

To illustrate the calculation required we set $n \cap r = 60$, $n \cap r' = 900$ and $r \cap n' = 40$, giving:

$$P(r|n) = \frac{(60/100) * (100/1000)}{((60/100) * (100/1000)) + ((900/900) * (900/1000))}$$

$$P(r|n) = 0.0625$$

The key piece of information required in the numerator is the prior knowledge about the prevalence of the rare species in the total dataset of TPP plots plus plots in which the neighbour species occurs, P(r). This probability is used to weight the probability that the neighbour species will be present given the rare species is present. Even if a neighbour species is very common the proportion of the total number of plots occupied by the neighbour and the rare species will be lower with increasing rarity of the rare species. The denominator equals P(n) and ensures that P(r|n) ranges between 0 and 1.

The probability of the neighbour occurring in plots where the rare species is absent, P(n|r'), is always 1 because all plots selected from the contextual datasets must have the neighbour present. This reflects our strategy for excluding plots where *both* rare species and neighbour are absent. These plots are uninformative because their joint absence provides no reliable information about the probability of the rare species occurring. With greater sampling of the rare species' range additional data may be justified for inclusion as additional neighbours are discovered accompanying the rare species. The other extreme would be to analyse the association between the neighbour and the rare species but only within plots where the rare species was present. This would ignore the many occurrences of the neighbour where the rare species was absent and thus overestimate the faithfulness of the neighbour.

Data assembly and analysis

For each of the six species, a list of neighbours was defined as any species that occurred in any of the TPP quadrat data for each species. To define the wider prevalence of the neighbours in the absence of the rare species we assembled quadrats from the datasets outlined in Table 1b where each neighbour occurred. This process yielded varying numbers of additional quadrats in which the rare species also occurred. These plots were added to the rare species dataset. Any species growing with the rarity in this dataset not already present in the TPP plots were also added to the list of neighbours.

Probabilities for each neighbour species (i.e. P(r|n)) were calculated in a SAS script (SAS Institute 1999). Mean probabilities were then calculated by natural log transforming and then averaging the probabilities across all neighbours occurring in each quadrat. Thus we calculated the geometric mean and thereby reduce the influence of any extreme values. This was done for the TPP plots and the wider GB survey plots in which the neighbour species occurred without the TPP species. The distribution of mean values for the TPP plots provides a reference distribution indicating the range of values likely in quadrats where the rarity occurs. The mean and range of probability values for the plots containing neighbours but without the rare species ought to be lower. Overlap indicates groups of TPP plots which could be considered sub-optimal or unoccupied patches elsewhere in GB that may provide favourable habitat for the rare species at least on the basis of the other species present.

Results

The mean number of neighbour species per TPP quadrat ranged from 53 for *Polystichum lonchitis* to 17 for *Astragalus danicus* (Table 2). The total number of neighbour species that were recorded at least once in quadrats with the rare species present ranged from 181 for *Vicia orobus* to 329 for *Gentianella campestris* but this difference in list length partly reflects differences in total number of quadrats recorded between TPP species (see Supplementary Material). Each of the TPP species was associated with a small number of neighbours that had probability values of 1, indicating that if the neighbour species is found then the TPP species will always be present (Fig. 2, Table 3). These probability values arise when the neighbour is present only in the TPP quadrats. Most reflect recording biases between the survey datasets. For example the critical *Euphrasia* taxa associated with *G. campestris* and *Blysmus compressus* were not differentiated in the wider contextual datasets. A small number of bryophyte species were also recorded in TPP quadrats and were either absent or under-recorded in the contextual data. For example, in the Countryside Survey only a limited range of common bryophytes are ever recorded.

Species with Bayes probability values less than 1 displayed very similar shaped distributions for each of the six TPP species. The majority of neighbour species had very low values, these being widespread plants found extensively in the absence of the TPP (Fig. 2). Those that occurred at least once with a TPP species but had the weakest associations were *Holcus lanatus, Agrostis capillaris, A. stolonifera, Poa trivialis, Lolium perenne, Galium saxatile, Calluna vulgaris, Trifolium repens* and *Nardus stricta*. A number of species had higher values thus exhibiting stronger associations with the TPP species (Fig. 2; Table 3). Many such species were very infrequent in the TPP data consistent with their extreme rarity in Britain. Hence their relatively high probabilities resulted from the fact that they were also very infrequent in the wider contextual datasets. For *A. danicus* these included *Dianthus deltoides*, *Neotinea ustulata* and *Orchis anthropophora*, all of which are very localised species of dry, infertile grasslands (Table 3). The strong but infrequent indicators for *G. campestris* reflected its relative abundance in very infertile swards in the north and west of the British Isles (*Gnaphalium sylvaticum*, *Meum athamanticum*, *Ophioglossum azoricum*) whereas for *Oenanthe fistulosa* its strongest neighbours were drawn from highly localised marsh and semi-aquatic assemblages (*Cicuta virosa*, *Hydrochoris morsus-ranae*, *Liparis loeselii*, *Sium latifolium*) (Table 3). The strong indicators for *Polystichum lonchitis* were by far the rarest reflecting the highly specialised and localised nature of its montane habitats (*Carex atrata*, *Draba norvegica*, *Dryopteris expansa*, *Saxifraga nivalis*, *Veronica fruticans*, *Woodsia ilvensis*). The relatively few strong indicators for *B. compressus* and *Vicia orobus* reflected the wide variety of habitats in which they were both recorded across both the TPP and contextual data (Table 3).

Discussion

Species diversity patterns and variation in numbers of neighbours

The total number of neighbour species differed between each TPP taxon. Three factors are important in shaping these differences. Sampling bias could interact with differences in the species richness of sampled plots (α-diversity) and species compositional turnover between plots (β-diversity) to influence the length of the list of neighbours. It is possible that the identification of neighbours was influenced by bias in the sampling procedure. However, this is more likely to have resulted from biased quadrat locations within each population location rather than biased selection of habitats. Sites containing populations of each species were randomly drawn in proportion to the number of known historical locations across vice-counties. Eligible locations were therefore distributed throughout the biogeographic range of each species and should unbiasedly represent the variation in occupied habitats and ecological conditions. However, within each location, quadrats were positioned to be representative of the rare species and its vegetation context rather than being strictly randomly placed. It is therefore possible that deliberate bias toward the rare species on each TPP site could increase the probability that any one neighbour occurs with the rare species. Yet this is precisely why we apply Bayes Theorem since this downweights the probability of the neighbour occurring given the presence of the rarity by the prevalence of the rare species in the wider UK dataset. The same could also be said for rare neighbours; targeting the rare TPP focal species could also have inflated the richness of rare species that are neighbours if rare species tend to grow together (Pilgrim *et al*., 2004). However rare species do not always occur together to produce hotspots of high rare species richness (Heegaard *et al*., 2013). Moreover, the average Bayes P values for the TPP plots are a function of all neighbour species, both common and rare. Hence the very high rare species probability values for the rarest species that grow with the TPP focal plant do not generally lead to very high average Bayes P values for TPP plots because these species are very rare in both the TPP and contextual data (Table 3).

Differences in the number and identity of neighbours will have also been influenced by variation in species composition between habitats and species richness within plots. Species compositional turnover will be greatest where the range of habitats and conditions varies across the species range and where the occupied habitats are typically species-rich. Turnover will be lower where the geographic range is smaller, where the same kind of habitat is occupied throughout the species range and where conditions limit the species richness of habitat patches. For example, relatively lower α-diversity could result from filtering for a small number of specialists such as salt-tolerant, shade-tolerant or montane taxa, or from the suppressive effect of a small number of dominants that thrive in the modern countryside (Pilgrim *et al.,* 2004; Smart *et al.,* 2006a). Given the trait profile of the declining plant species in Britain and NW Europe - typically short, stress-tolerant forbs at a competitive disadvantage under high nutrient supply and when competing for light - the former scenario would seem more likely to apply to vegetation with low α-diversity but containing rare species (see for example Lauterbach *et al.,* 2013; Powney *et al.,* 2014; Walker & Preston 2006; Tamis *et al.,* 2005; Braithwaite *et al.,* 2006; Smart *et al.,* 2006b; Sundberg 2014). In fact α-diversity varied considerably across each species dataset (Table 2).When differences in the total number of TPP plots were taken into account, the count of neighbours was relatively low for *Vicia orobus* whereas *Polystichum lonchitis* had a somewhat longer list of neighbours than expected given the number of TPP plots recorded. To help assess the contribution of within-plot species richness versus turnover between plots, we calculated β-diversity as the total number of associates divided by mean species richness (Anderson *et al.,* 2011). This metric takes into account species richness in plots to give the number of different species that need on average to be present in each plot to yield the total pool of neighbours recorded across all plots. It is, therefore, an estimator of average turnover in species composition between plots.

The greatest β-diversity was attributable to *Astragalus danicus* (Table 2). In the TPP surveys, this species was found in a wide range of habitats from sea level to 710m, in coastal heath, dune grassland, neutral grassland, road verges and calcareous grassland, the common denominator being short vegetation height, typically <10cm, and either level-or south-facing slopes (Walker 2011). The lowest β-diversity was associated with *Polystichum lonchitis,* reflecting its confinement to a much narrower range of conditions; typically calcareous high altitude rock outcrops, screes and limestone pavement, but where species richness within plots was the greatest of the six species studied (Table 2).

Applying neighbour species to newly recorded vegetation

Our method for deriving indicator species has advantages and disadvantages. We calculated the probability of a rare species being present given the presence of another neighbour species, but did not account for further multi-species associations for example where rare species A has a greater or lesser probability of occurring if neighbour X is also joined by neighbour Y. Thus the disadvantage of this strictly individualistic approach is that it does not explicitly include multiple inter-specific associations of the kind that would emerge from ordination or community distribution models (Chapman & Purse 2011). Hill (1989) mooted the idea of applying Bayes theorem to the assignment of new species lists to existing probabilistic classifications of plant communities. However, he saw the challenge of including all possible multiple species dependencies as insurmountable. Since we were interested in determining the indicator status of each neighbour species independently of any other, Bayes theorem could still be applied. There are a number of advantages: Since each species-specific Bayes probability value is treated as independent of any other then they are also independent of recording biases in the data. Thus the *Gentianella campestris* Bayes probability value for its neighbour *Spiranthes spiralis* is not influenced by the under-recording of *Euphrasia* taxa in the contextual data. In addition, it would also be possible to apply a pre-selected subset of "easier-to-identify" indicators, for example in a citizen science field campaign such as the new National Plant Monitoring Scheme, where botanical skill varies among volunteers. Not recording the entire species composition of quadrats would weaken the power of the approach, but not invalidate it.

Having calculated Bayes probabilities for each neighbour, the database of values can be used to generate reference distributions of mean Bayes probabilities for both (1) the TPP data, in which the rare species was always recorded (less negative values, Fig. 3) and (2) the contextual data, representing the range of every neighbour species but where the TPP species was absent (more negative values, Fig. 3). These distributions allow mean probability values for new quadrat species lists to be evaluated graphically and statistically. Questions might include, how does the mean indicator value for *Astragalus danicus* calculated from new monitoring plots, or from vegetation in which *A. danicus* was recorded previously, compare to the distribution of values for TPP plots in which *A. danicus* was present? Thus, the database of probability values can be applied to new quadrat species lists. There is no need to further discriminate indicators from non-indicators based on the size of the probability value. All the associate species carry information, and all can be applied. If associates with higher probability values are present, this will simply increase the mean value for a new species list. A quadrat from the *Blysmus compressus* TPP dataset was selected to illustrate this approach. The species list was recorded in a 1x3m quadrat centred on a population of c.100 individuals confined to the shorter vegetation at the edge of the verge on the Orton to Appleby road in Cumbria (OS grid reference NY 646 156 (lat 54.534426 long -2.5485796)) (Plates 1 & 2). Six species; *Matricaria discoidea, Potentilla anserina, Puccinellia distans, Polygonum aviculare, Agrostis stolonifera* and *Poa annua* were recorded with *B. compressus*. The mean of the natural log of the Bayes probabilities for these four species is -4.87. A statistical test of the probability of this value being more negative than a random draw from the population of Bayes values can be carried out using a simple randomisation test where the value is compared with 1000 bootstrapped samples drawn from the reference dataset (Philippi *et al.,* 1998). An R function to perform the test and to plot the observed value against the associated reference distribution for each of the six species (Fig. 1S) is available from the corresponding author on request and in Supplementary Material. The test gave a probability value of 0.001 indicating a very small chance of the observed mean being less than a random draw. Therefore, despite being a relatively species-poor quadrat in the context of all *Blysmus*-containing vegetation (mean species richness =24 $1m^{-2}$; Table 2), the suite of neighbours growing with *B. compressus* at this location did not suggest an unfavourable floristic context for the threatened species population. The position of the new assemblage to the right of the reference distribution does however suggest a less typical mix of species yet this is not attributable to the presence of a large number of widespread species. While this simple test is robust to non-normal reference distributions, interpretation still requires caution because the survey datasets used to build the reference distributions cannot be considered totally unbiased samples of the vegetation in which neighbours and rare species occur.

A further issue to consider is that species lists from newly surveyed patches of vegetation may contain species that were never recorded in TPP plots (Fig. 1). These could be considered negative indicators, yet there is no obvious way of quantifying their negative association sensibly other than to simply present a count of such species. Labelling these species as negative indicators also assumes that they never occur with the rare species yet their discovery alongside the rarity immediately classes them as neighbours. The most we can say without further trait-based analysis is that species with very low Bayes probability values are not restricted to the conditions associated with the rare plant and so may in fact be indicators of unfavourable conditions.

Modelling changes in rare species by modelling their neighbours

Information about the conditions associated with the rare species can be inferred from their neighbours. Where these are widespread species their traits and abiotic preferences can be easily obtained. For example, associated disturbance regime, degree of habitat specialisation, substrate fertility, wetness and pH can be estimated from existing plant attribute databases (e.g. Hodgson 1991; Lewis *et al.,* 2014). However, an emerging possibility involves the use of empirical niche models applied to the neighbour species. An advantage, over and above simple averaging of trait information, is that interactions among environmental predictors are explicitly included and quantify for example how a plant species' response to soil fertility is modified by soil wetness or successional status (Pakeman *et al.,* 2008; Henrys *et al.,* in press). These models can be used to project the impact of environmental change on plant species composition driven by external factors such as climate or along abiotic gradients that can be influenced by management such as vegetation height, pH and ground wetness (Henrys *et al.,* in press). The impact on habitat suitability for the rare species may then be estimated by recalculating mean Bayes probabilities as neighbour species composition undergoes simulated change. As neighbour species composition changes so will the mean Bayes values associated with the rare species thus quantitatively linking changing ecological conditions to the fortunes of rare plant species populations via the modelled responses of neighbouring plants. Linkage between habitat suitability indices for neighbours and those for rare species could be formally realised within a Bayesian Belief Network (Jensen, 1996). Whilst such simulations of the impacts of environmental change are increasingly possible at the habitat patch scale, the application of empirical niche models often relies on the assumption that patterns in space can usefully substitute for changes in time. This becomes questionable the more that projections are based on novel configurations of environmental conditions (Thuiller *et al.,* 2008; Williams & Jackson 2007).

Further applications

Application of the neighbour-species method is ultimately data constrained. Indeed the examples presented here have only become possible with the availability of the TPP survey data. Even so, both temporal and spatial biases are inherent in the wider survey data and in the extent to which rare species' niche space is accurately represented in the rare species data. We suggest that the best way to understand and minimise the impacts of these sources of variation is to apply the method dynamically so that neighbour lists and their Bayes probabilities are allowed to change and potentially stabilise as more data is collected. Because the calculations are so simple, new rare species survey data uploaded to an on-line repository could be routinely and rapidly processed to update the list of neighbours and associated Bayes probability values and the range of conditions associated with each new rare species population or extirpated population. The uptake of the TPP by volunteer plant recorders suggests that this could be a popular initiative within the biological recording community.

Acknowledgements

We thank Martin Rand, Sue Townsend, Paul Smith and two anonymous referees for insightful comments that helped improved the manuscript. The authors acknowledge and thank the many vice-county recorders and volunteers who collected the TPP survey data. The Key Habitats Survey, Countryside Surveys and GB Woodland Surveys have been funded by consortia of government and non-government bodies including the Department of the Environment, Food and Rural Affairs, the Natural Environment Research Council. Natural England, Scottish Natural Heritage, Natural Resources Wales, Forestry Commission, Joint Nature Conservation Committee and the Woodland Trust.

Supplementary material

Fig 1S: Graphical output from the R function that conducts a randomisation test of the probability that the mean ln(Bayes probability) for neighbour species in a new patch is more negative than a random draw from the reference distribution for any of the six TPP species. The histogram shows the distribution of mean ln(Bayes probabilities) for the TPP quadrat dataset for *Blysmus compressus* and the position (dashed line) of the example value of -4.87. See text.

S2_TPP_randomisation_test.txt : An R script to carry out a randomisation test for newly recorded vegetation data and to generate the graph shown in Fig 1S.

S3_All_scores.xlsx: Mean ln(Bayes probabilities for each TPP plot). Required to carry out the randimsation test and generate the reference distribution.

S4_TPP_neighbour_list.xlsx : List of Bayes probability values and count data for all neighbour species.

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FIGURES & TABLES

Table 1a: Survey data pertaining to the six rare species selected from the BSBI Threatened Plant Project (TPP). See http://www.bsbi.org.uk/tpp.html for further details.

Species	Number of locations surveyed	Number of locations where species was found	Number of recorded quadrats containing the rare species
Astragalus danicus	106	75	83
Blysmus compressus	111	88	102
Gentianella campestris	205	149	160
Oenanthe fistulosa	121	82	113
Polystichum lonchitis	54	46	51
Vicia orobus	111	75	96

Table 1b: Survey data used to represent the wider British ecological range of neighbour species associated with the six TPP species. All datasets except the NVC were extracted from databases maintained at the NERC Centre for Ecology & Hydrology (CEH), Lancaster.

Dataset	Reference	Date recorded	Geographical scope	Source	Number of quadrats
National Vegetation Classification	Rodwell (1997) et seq.	1965-1980	Great Britain	I.M. Strachan (JNCC)	31266
Countryside Survey 2000	Smart et al. (2003)	1998/1999	Great Britain	CEH	7221
Key Habitats survey	Hornung et al. (1996)	1995	Great Britain	CEH	548
The 'Bunce' Woodland Survey	Kirby et al. (2005)	1971	Great Britain	CEH	1648

Table 2: Summary of species composition and diversity of the TPP quadrats (2m diameter circular plots).

TPP species	**Count of associated species**	**Count of associated bryophytes**	**Mean species richness and range per quadrat**	**Beta diversity**
Astragalus danicus	278	1	17.14 (3-84)	16.22
Blysmus compressus	262	25	24 (4-42)	10.92
Gentianella campestris	329	13	35.12 (4-143)	9.37
Oenanthe fistulosa	301	7	24.54 (1-82)	12.27
Polystichum lonchitis	230	1	53.24 (1-167)	4.32
Vicia orobus	181	4	17.51 (1-36)	10.34

Fig 1: Conceptual distributions of species along an arbitrary niche axis. A rare species (r) occupies a narrow range of conditions and is less common than a more wide-ranging neighbour species (n) with which it coexists (n+r) in a part of their joint ecological range. A non-neighbour (nn) species never grows with the rare species and so species presence data from this part of the niche axis is excluded from the analysis of the association between neighbour (n) and rare species (r).

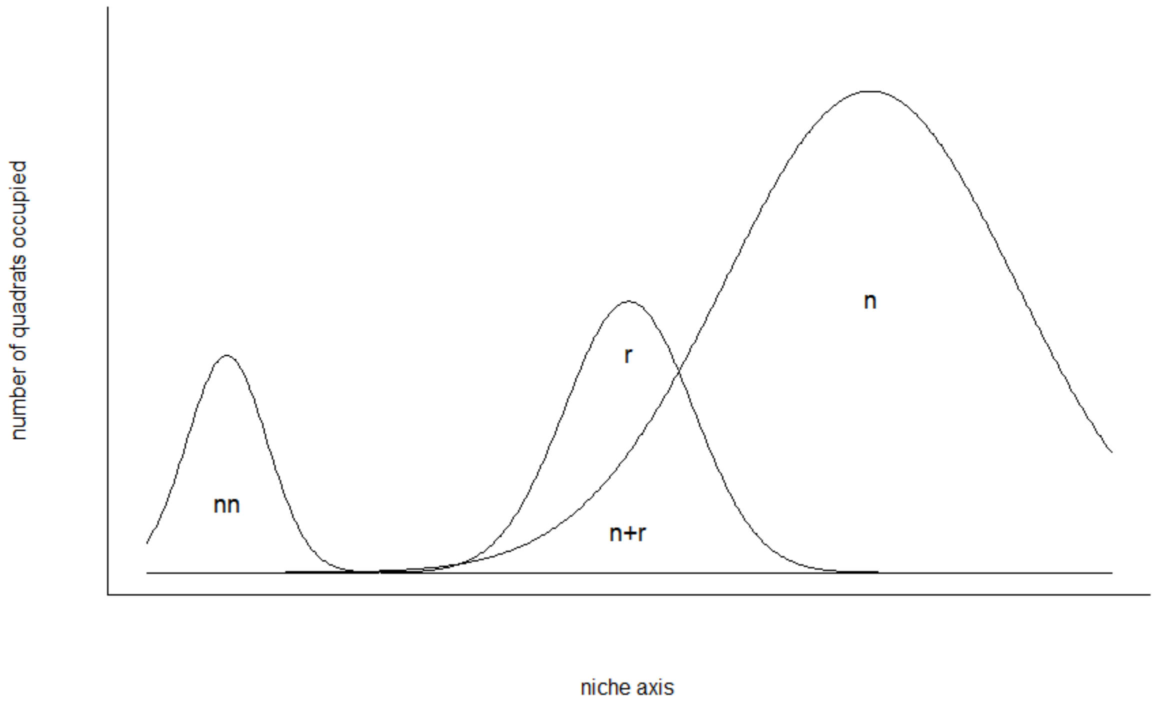

Fig 2: Histograms of Bayes probability values for neighbour species associated with (a) *Astragalus danicus*, (b) *Vicia orobus*, (c) *Blysmus compressus*, (d) *Gentianella campestris*, (e) *Oenanthe fistulosa* and (f) *Polystichum lonchitis*. In each graph probabilities are grouped into 50 equal intervals on the X axis between 0 and 1.

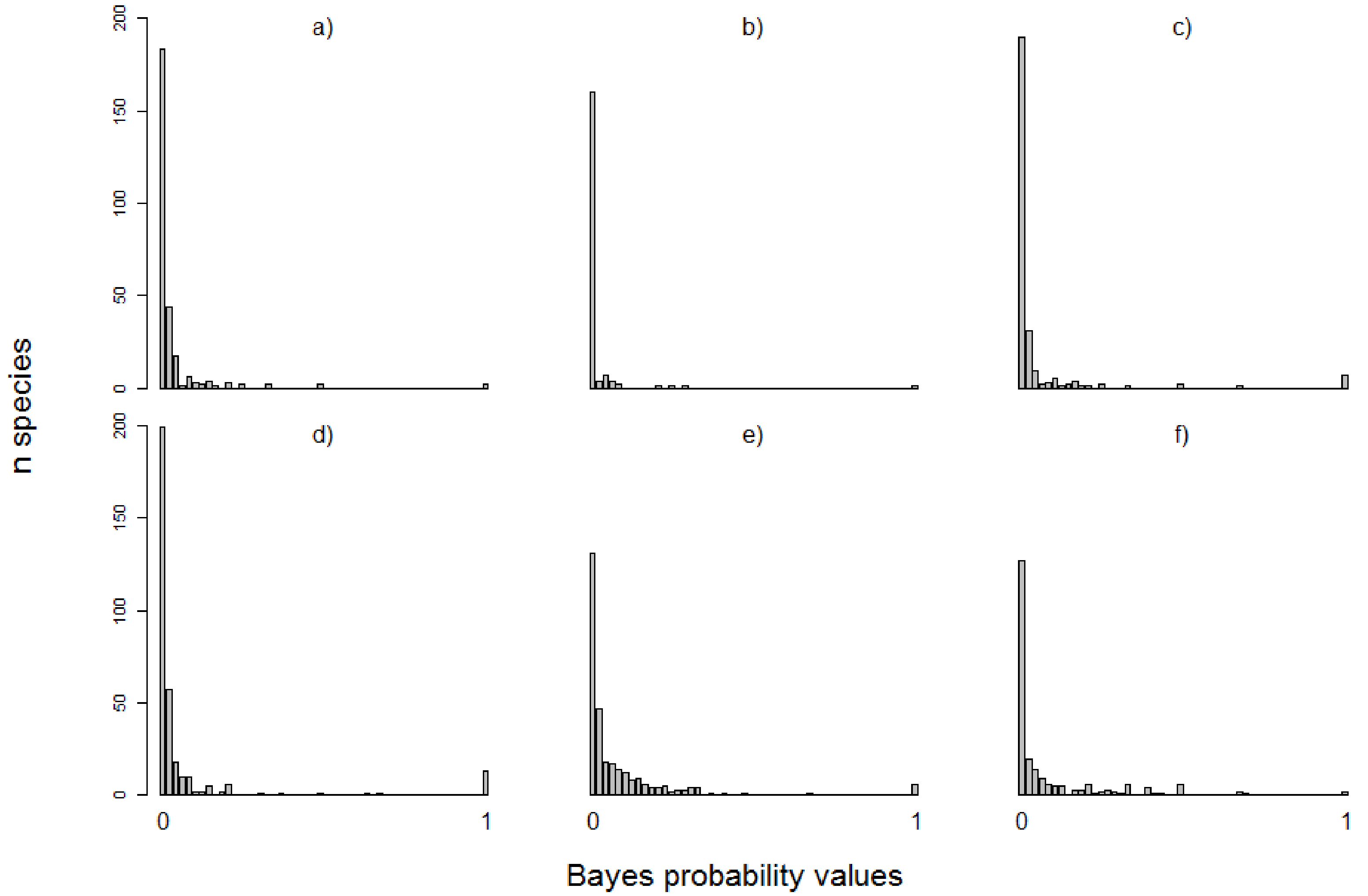

Fig 3: Distributions of mean (log$_e$ transformed Bayes probability values) for 6 plant species datasets either where the rare TPP species was recorded (Rare present) or where the rare species was absent but where all plots contained at least one record for a neighbour species growing at least once with the rare species in the TPP dataset. (a) *Astragalus danicus*, (b) *Vicia orobus*, (c) *Blysmus compressus*, (d) *Gentianella campestris*, (e) *Oenanthe fistulosa* and (f) *Polystichum lonchitis*.

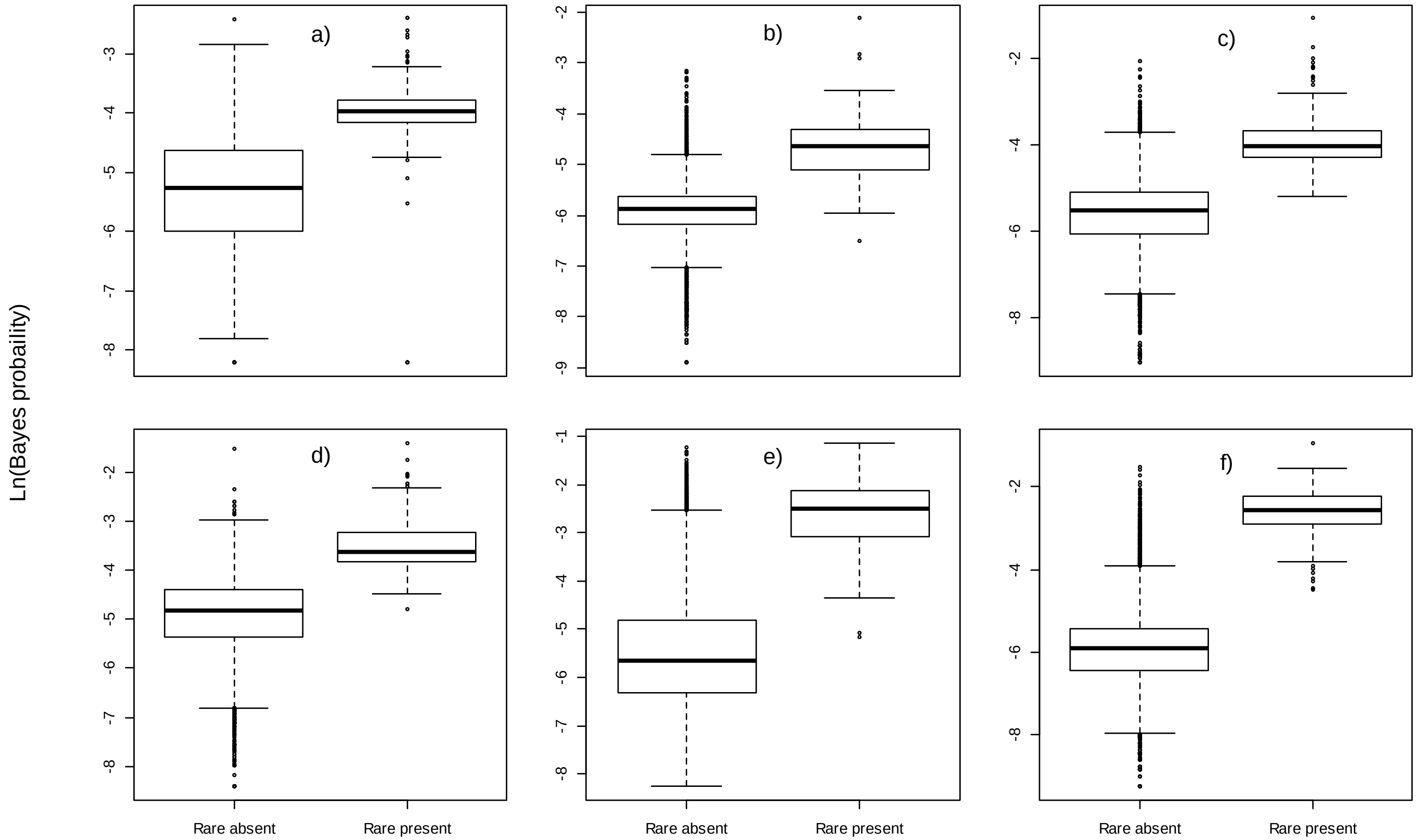

Fig 1S: Graphical output from the R function that conducts a randomisation test of the probability that the mean ln(Bayes probability) for neighbour species in a new patch is more negative than a random draw from the reference distribution for any of the six TPP species. The histogram shows the distribution of mean ln(Bayes probabilities) for the TPP quadrat dataset for *Blysmus compressus* and the position (dashed line) of the example value of -4.87. See text.

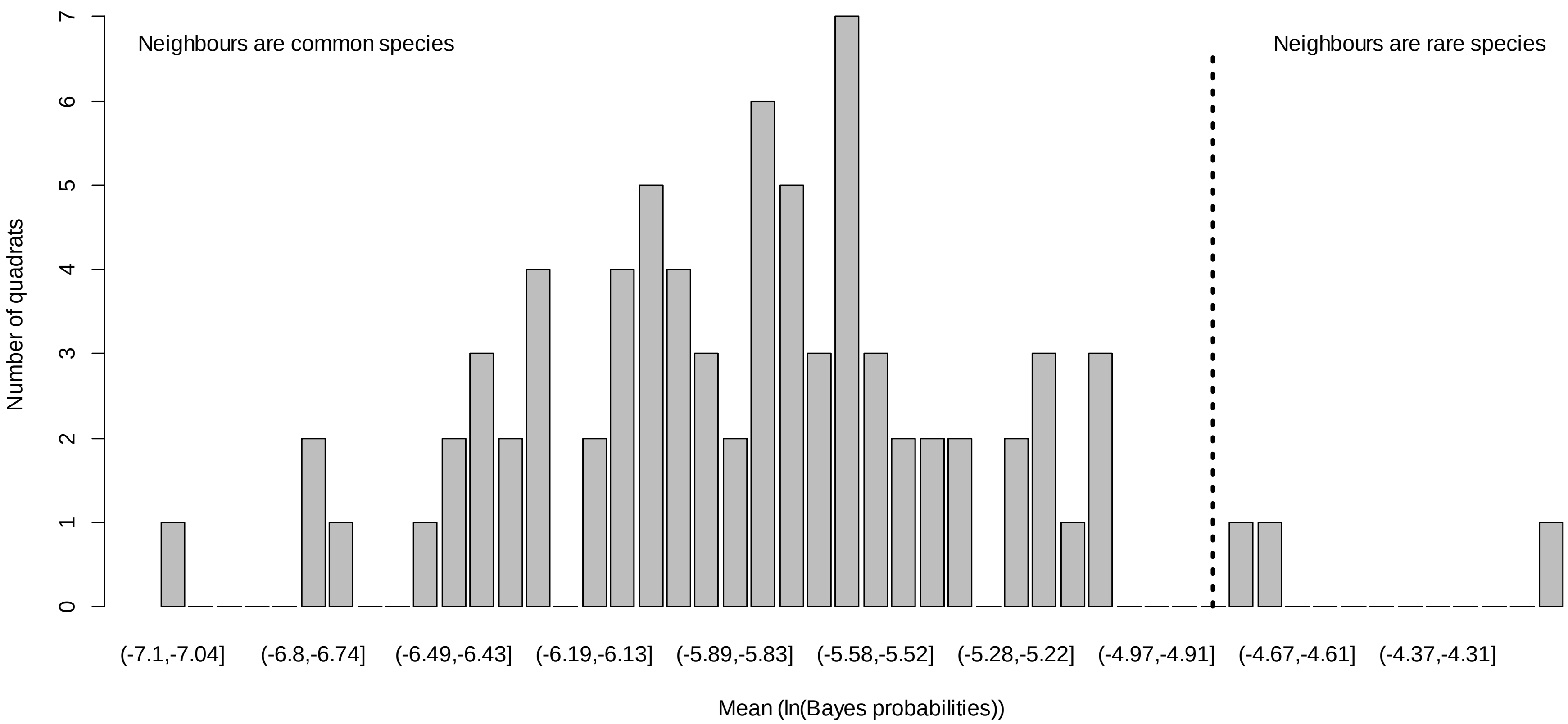

Table 3: Neighbour species for six species surveyed in the BSBI Threatened Plants Project (TPP). Species that only occurred in the TPP quadrat data have a Bayes probability value of 1. For indicator species that also occurred in the absence of the TPP species in wider GB survey data, the top 40 most faithful neighbours are listed. See Supplementary Material for a complete list. Species counts used to calculate the Bayes probabilities are shown in three columns.

TPP species	Indicator species	TPP data Rare present, Neighbour present	TPP data Rare present, Neighbour absent	Contextual data Rare absent, Neighbour present	Bayes_P
Astragalus danicus	*Anagallis minima*	1	182	0	1.000
	Potentilla tabernaemontani	1	182	1	0.500
	Dianthus deltoides	3	180	3	0.500
	Neotinea ustulata	2	181	4	0.333
	Orchis anthropophora	1	182	2	0.333
	Erophila verna sens.lat.	2	181	6	0.250
	Stellaria pallida	1	182	3	0.250
	Cirsium eriophorum	5	178	20	0.200
	Ophrys insectifera	3	180	12	0.200
	Dactylorhiza purpurella	1	182	4	0.200
	Arenaria serpyllifolia	4	179	19	0.174
	Anacamptis morio	3	180	16	0.158
	Ophrys apifera	4	179	22	0.154
	Carex ericetorum	2	181	12	0.143
	Filago vulgaris	1	182	6	0.143
	Alchemilla filicaulis	1	182	7	0.125
	Pulsatilla vulgaris	12	171	85	0.124
	Saxifraga granulata	4	179	32	0.111
	Rubus caesius	1	182	8	0.111
	Anacamptis pyramidalis	4	179	33	0.108
	Cerastium arvense	5	178	46	0.098

	Thesium humifusum	5	178	47	0.096
	Arabis hirsuta	5	178	51	0.089
	Echium vulgare	6	177	63	0.087
	Viola odorata	7	176	77	0.083
	Poa humilis	3	180	34	0.081
	Descurainia sophia	1	182	15	0.063
	Claytonia perfoliata	1	182	16	0.059
	Viola canina	15	168	243	0.058
	Genista tinctoria	3	180	49	0.058
	Reseda lutea	3	180	49	0.058
	Sherardia arvensis	3	180	49	0.058
	Rosa spinosissima	7	176	116	0.057
	Geranium sanguineum	9	174	151	0.056
	Coeloglossum viride	5	178	85	0.056
	Juncus balticus	1	182	18	0.053
	Tragopogon pratensis	6	177	110	0.052
	Carlina vulgaris	17	166	353	0.046
	Vulpia bromoides	3	180	64	0.045
	Knautia arvensis	5	178	107	0.045
	Tephroseris integrifolia subsp. *integrifolia*	2	181	44	0.043
Blysmus compressus	*Didymodon insulanus*	1	114	0	1.000
	Bryum pallens	1	114	0	1.000
	Hygrohypnum ochraceum	1	114	0	1.000
	Euphrasia scottica	1	114	0	1.000
	Euphrasia confusa	2	113	0	1.000
	Euphrasia nemorosa	2	113	0	1.000
	Dactylorhiza incarnata	7	108	0	1.000
	Dactylorhiza praetermissa	4	111	2	0.667

Brachythecium rivulare	1	114	1	0.500
Marchantia polymorpha	1	114	2	0.333
Plagiomnium rostratum	2	113	6	0.250
Isolepis setacea	9	106	35	0.205
Salix repens agg.	10	105	44	0.185
Climacium dendroides	4	111	20	0.167
Salix phylicifolia	3	112	15	0.167
Bryum pseudotriquetrum	1	114	5	0.167
Cratoneuron filicinum	1	114	5	0.167
Scorpidium revolvens	2	113	11	0.154
Conocephalum conicum	1	114	6	0.143
Philonotis fontana	2	113	14	0.125
Palustriella commutata	2	113	16	0.111
Tortella tortuosa	1	114	8	0.111
Glyceria notata	5	110	42	0.106
Campylium stellatum	1	114	9	0.100
Puccinellia distans	1	114	9	0.100
Rhinanthus minor	7	108	68	0.093
Trifolium fragiferum	2	113	21	0.087
Primula farinosa	7	108	79	0.081
Triglochin palustre	22	93	320	0.064
Sagina nodosa	8	107	127	0.059
Juncus inflexus	29	86	473	0.058
Homalothecium lutescens	1	114	18	0.053
Juncus balticus	1	114	18	0.053
Pulicaria dysenterica	9	106	197	0.044
Epilobium parviflorum	10	105	219	0.044
Juncus articulatus	60	55	1353	0.042
Eleocharis quinqueflora	10	105	231	0.041
Carex hirta	19	96	455	0.040

	Eleocharis palustris	16	99	387	0.040
	Carex disticha	13	102	319	0.039
	Veronica beccabunga	9	106	227	0.038
	Calliergonella cuspidata	11	104	278	0.038
	Brachythecium rutabulum	2	113	51	0.038
	Veronica anagallis-aquatica	1	114	26	0.037
	Cardamine pratensis	17	98	453	0.036
Gentianella campestris	*Didymodon fallax*	1	233	0	1.000
	Pseudocrossidium revolutum	1	233	0	1.000
	Fissidens osmundoides	1	233	0	1.000
	Phascum cuspidatum	1	233	0	1.000
	Racomitrium aciculare	1	233	0	1.000
	Weissia controversa	1	233	0	1.000
	Euphrasia officinalis subsp. *anglica*	1	233	0	1.000
	Euphrasia salisburgensis	1	233	0	1.000
	Euphrasia scottica	1	233	0	1.000
	Euphrasia tetraquetra	2	232	0	1.000
	Euphrasia micrantha	5	229	0	1.000
	Euphrasia confusa	6	228	0	1.000
	Euphrasia nemorosa	6	228	0	1.000
	Meum athamanticum	2	232	1	0.667
	Gnaphalium sylvaticum	5	229	3	0.625
	Ophioglossum azoricum	1	233	1	0.500
	Alchemilla filicaulis	4	230	7	0.364
	Spiranthes spiralis	3	231	7	0.300
	Botrychium lunaria	15	219	55	0.214
	Alchemilla alpina	9	225	33	0.214

Rhinanthus minor	18	216	68	0.209
Salix repens	11	223	44	0.200
Dactylorhiza purpurella	1	233	4	0.200
Parentucellia viscosa	1	233	4	0.200
Carex rupestris	4	230	17	0.190
Potentilla crantzii	6	228	33	0.154
Carex capillaris	15	222	90	0.143
Chamaemelum nobile	2	232	12	0.143
Filago vulgaris	1	233	6	0.143
Veronica fruticans	1	233	6	0.143
Potentilla anglica	2	232	13	0.133
Primula scotica	5	229	36	0.122
Coeloglossum viride	11	223	87	0.112
Campylium stellatum	1	233	9	0.100
Equisetum variegatum	7	227	64	0.099
Galium sterneri	25	217	241	0.094
Daucus carota	6	228	60	0.091
Carex maritima	1	233	10	0.091
Radiola linoides	1	233	10	0.091
Dryas octopetala	7	227	71	0.090
Sagina saginoides	1	233	11	0.083
Persicaria vivipara	41	205	459	0.082
Salix reticulata	3	231	34	0.081
Tofieldia pusilla	5	229	58	0.079
Alchemilla glabra	3	231	35	0.079
Galium boreale	8	226	101	0.073
Betula pubescens	7	227	89	0.073
Antennaria dioica	19	215	252	0.070
Sesleria caerulea	14	220	192	0.068
Vicia sylvatica	1	233	14	0.067

	Trifolium medium	7	227	102	0.064
	Saxifraga aizoides	20	217	292	0.064
Oenanthe fistulosa	*Calliergon cordifolium*	1	246	0	1.000
	Drepanocladus aduncus	1	246	0	1.000
	Amblystegium riparium	1	246	0	1.000
	Euphrasia nemorosa	1	246	0	1.000
	Wolffia arrhiza	1	246	0	1.000
	Rorippa nasturtium-aquaticum sens.str.	4	243	0	1.000
	Liparis loeselii	6	241	3	0.667
	Hydrocharis morsus-ranae	8	239	9	0.471
	Sium latifolium	17	230	24	0.415
	Cicuta virosa	21	226	36	0.368
	Carex pseudocyperus	28	219	55	0.337
	Alopecurus aequalis	1	246	2	0.333
	Dipsacus pilosus	1	246	2	0.333
	Lathyrus palustris	12	235	25	0.324
	Ranunculus lingua	33	214	73	0.311
	Elodea nuttallii	4	243	9	0.308
	Oenanthe aquatica	3	244	7	0.300
	Rorippa palustris	3	244	7	0.300
	Stellaria palustris	28	219	70	0.286
	Spirodela polyrhiza	4	243	10	0.286
	Butomus umbellatus	2	245	5	0.286
	Carex appropinquata	24	223	62	0.279
	Veronica catenata	7	240	19	0.269
	Berula erecta	57	190	157	0.266
	Eleocharis acicularis	1	246	3	0.250
	Epilobium roseum	1	246	3	0.250

	Thyselium palustre	60	187	195	0.235
	Carex elata	55	192	180	0.234
	Hottonia palustris	3	244	10	0.231
	Lemna trisulca	12	235	41	0.226
	Rumex hydrolapathum	37	210	129	0.223
	Myriophyllum verticillatum	3	244	12	0.200
	Lemna minuta	2	245	8	0.200
	Azolla filiculoides	1	246	4	0.200
	Cotoneaster simonsii	1	246	4	0.200
	Ranunculus trichophyllus	4	243	17	0.190
	Impatiens capensis	7	240	30	0.189
	Potamogeton coloratus	3	244	13	0.188
	Rorippa amphibia	2	245	9	0.182
	Sagittaria sagittifolia	4	243	19	0.174
	Lysimachia vulgaris	54	193	258	0.173
	Calamagrostis canescens	33	214	158	0.173
	Cladium mariscus	53	195	269	0.165
	Typha angustifolia	18	229	92	0.164
	Schoenoplectus lacustris	8	239	41	0.163
	Carex lasiocarpa	21	226	114	0.156
Polystichum lonchitis	*Arabis alpina*	1	83	0	1.000
	Woodsia alpina	1	83	0	1.000
	Saxifraga nivalis	7	80	3	0.700
	Dryopteris expansa	2	82	1	0.667
	Draba norvegica	6	81	3	0.667
	Pellia epiphylla	1	83	1	0.500
	Pseudorchis albida	1	83	1	0.500
	Woodsia ilvensis	1	83	1	0.500

Carex atrata	15	73	16	0.484
Veronica fruticans	3	81	4	0.429
Alchemilla alpina	23	61	33	0.411
Draba incana	17	72	26	0.395
Asplenium viride	32	56	50	0.390
Oxyria digyna	35	57	55	0.389
Poa glauca	5	80	8	0.385
Cystopteris montana	1	83	2	0.333
Angelica sylvestris	1	83	2	0.333
Astragalus alpinus	1	83	2	0.333
Carex norvegica	1	83	2	0.333
Erigeron borealis	1	83	2	0.333
Saussurea alpina	25	64	52	0.325
Arabidopsis petraea	5	80	11	0.313
Cerastium alpinum	12	74	29	0.293
Carex vaginata	7	78	17	0.292
Poa alpina	5	80	13	0.278
Saxifraga oppositifolia	42	50	115	0.268
Cystopteris fragilis	23	64	65	0.261
Potentilla crantzii	10	76	30	0.250
Salix reticulata	9	77	28	0.243
Galium boreale	27	64	87	0.237
Sedum rosea	39	54	143	0.214
Salix lapponum	9	79	35	0.205
Arabis hirsuta	11	74	44	0.200
Salix lanata	3	81	12	0.200
Vicia sylvatica	3	81	12	0.200
Salix arbuscula	2	82	8	0.200
Dryas octopetala	15	71	64	0.190
Alchemilla glabra	8	76	35	0.186

	Carex rupestris	4	80	18	0.182
	Pyrola rotundifolia	10	74	49	0.169
Vicia orobus	*Ajuga pyramidalis*	1	99	3	0.250
	Cotoneaster simonsii	1	99	4	0.200
	Rhinanthus minor	7	93	68	0.093
	Lathyrus linifolius	33	67	357	0.085
	Potentilla anglica	1	99	13	0.071
	Platanthera chlorantha	1	99	14	0.067
	Salix repens	3	97	44	0.064
	Hypericum maculatum	1	99	15	0.063
	Trifolium medium	6	94	104	0.055
	Genista tinctoria	3	97	52	0.055
	Stachys officinalis	29	71	598	0.046
	Carex pallescens	4	96	91	0.042
	Polypodium vulgare sens.str.	4	96	92	0.042
	Vicia sativa	2	98	48	0.040
	Hieracium sp.	7	93	171	0.039
	Platanthera bifolia	1	99	28	0.034
	Asplenium adiantum-nigrum	1	99	42	0.023
	Salix aurita	3	97	143	0.021
	Brachythecium rutabulum	1	99	51	0.019
	Teucrium scorodonia	15	85	855	0.017
	Rosa spinosissima	2	98	121	0.016
	Hypericum pulchrum	11	89	668	0.016
	Lonicera periclymenum	6	94	368	0.016
	Stellaria graminea	7	93	460	0.015
	Sanguisorba officinalis	8	92	532	0.015
	Solidago virgaurea	7	93	466	0.015
	Serratula tinctoria	6	94	412	0.014

Torilis japonica	2	98	141	0.014
Conopodium majus	15	85	1067	0.014
Dactylorhiza maculata	2	98	162	0.012
Lapsana communis	2	98	169	0.012
Centaurea nigra	32	68	2937	0.011
Populus tremula	1	99	95	0.010
Gymnadenia conopsea sens.lat.	2	98	207	0.010
Galium boreale	1	99	108	0.009
Asplenium trichomanes	1	99	111	0.009
Arrhenatherum elatius	27	73	3027	0.009
Cytisus scoparius	1	99	113	0.009
Aira caryophyllea	2	98	227	0.009