Complementarity analysis: Mapping the performance of surrogates for biodiversity

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\textbf{ABSTRACT}

Efficient planning for biodiversity conservation requires a consideration of complementarity when assessing the value of adding new areas for management. Unfortunately, complementarity in biodiversity across all groups cannot usually be measured directly, so methods are needed to choose good surrogates (or ‘indicators’) for predicting this overall complementarity. Previous attempts at assessment of biological surrogates have measured dissimilarity among biotas, or congruence between sets of selected areas, or species representation within a set of selected areas, all of which can seriously misrepresent the strength of a surrogate relationship across all areas. Therefore, we propose a new approach to complementarity analysis. We show that the pattern of complementarity among all biotas can be assessed in terms of the frequency of false high and false low predictions by the surrogates. We also show how the spatial pattern in these false predictions can be mapped and discuss their usefulness. On the one hand, areas on these maps associated with many false high predictions are overvalued and would be an inefficient investment for scarce conservation resources. On the other hand, areas associated with many false low predictions are undervalued and unlikely to attract conservation action, so we need to know whether they are particularly likely to be highly threatened. These geographical patterns can be used to identify habitat-associated biases in the performance of surrogate groups.

\section{Introduction}

Conservation scientists have called for methods to identify good surrogates for biodiversity in order to facilitate efficient conservation planning (e.g., Gaston and Williams, 1993; Kremen et al., 1993; Prendergast et al., 1993a; Reid et al., 1993; Pearson, 1994; Williams and Gaston, 1994; Samways et al., 1995; Faith and Walker, 1996b; Margules and Pressey, 2000; Araujo et al., 2004; Kati et al., 2004; Saetersdal et al., 2004; Trakhtenbrot and Kadmon, 2005). The need for efficiency arises from a desire to counter the recent increase in the rate of biodiversity loss (Convention on Biological Diversity: Anonymous, 1994) while still seeking to meet society’s other needs. To assess whether particular options for conservation are cost-effective as part of the decision-making process, quantitative and accountable methods are needed.
1.1. Surrogates

Part of the problem is that there is too much biodiversity in the world for us to be able to measure all of it directly. Therefore, we have to rely on surrogates (or ‘indicators’) that are well known, or relatively inexpensive to survey, and that can act as proxies for broader biodiversity value within the conservation-planning process (e.g., Reid et al., 1993). In the context of planning for conserving biodiversity in networks of managed areas, in order to achieve efficiency, it is biotic complementarity among areas that is important. Consequently a key question is: how to assess potential surrogates as good or bad predictors of the complementarity within broader biodiversity?

1.2. Complementarity

Complementarity exists when an area has at least some biodiversity features (species in the current context) or pattern that are unrepresented in some other area with which the area is being compared (Vane-Wright et al., 1991; Faith and Walker, 1996c; Williams, 2001; Faith et al., 2003). For example, a patch of grassland and a patch of forest might each be expected to have a higher number of different and complementary species (and so will represent more species in combination) than would two different patches within the same kind of grassland. Complementarity is a special case of the broader idea in land-use planning of marginal value, which is the incremental gain accrued when an area is managed in a particular way as part of a land management plan.

Maximising complementarity allows us to identify important areas for conservation that can add as much biodiversity as possible to a plan. Therefore, the relevant surrogacy question for conservation is not whether the pattern of species richness within one group predicts the pattern of richness within another group. Instead, we need to know whether complementarity within a surrogate group is predictive of complementarity within another group, or within biodiversity in general (Williams, 1993; Faith and Walker, 1996c; Gaston, 1996; Howard et al., 1998).

1.3. Previous studies assessing surrogates for complementarity

There have been few previous attempts to assess the value of surrogates as predictors of complementarity within biodiversity, and those attempts that have been made have substantial flaws or limitations.

First, some authors have claimed that complementarity is a kind of dissimilarity, and have used symmetrical dissimilarity metrics, particularly Bray-Curtis, as a measure of complementarity (e.g., Colwell and Coddington, 1994; Howard et al., 1998; Lund and Rahbek, 2002; Moore et al., 2003). This approach is seriously flawed, because complementarity between pairs of biotas is usually asymmetrical and may be strongly so. For example, a small coastal island may have only a small subset of the biota of the neighbouring mainland, without additional species. In this case, the mainland has high complementarity with respect to the island, but the island has no complementarity with respect to the mainland.

Another common weakness of this first approach is that using the mean (or median) value for a complementarity measure to assess prediction between groups could be misleading. For example, consider a plot of the kind shown in Fig. 1, which shows a scatterplot of complementarity scores (numbers of complementary species of birds, x, and plants, y) for pairs of areas. If Fig. 1 had similar ranges of values on both axes, and if the complementarity values were concentrated both near the origin and in the upper left and lower right corners, but not in the middle, then mean (or median) complementarity for the two groups could be very similar, even though true prediction of complementarity would be very poor (with most predictions being falsely high or falsely low, see below).

A second approach has been to apply complementarity-based area selection to both a surrogate and the group to be predicted and then examine the spatial overlap between the two area sets (e.g., Saetersdal et al., 1993; Dobson et al., 1997; Jaarsveld et al., 1998; Reyers et al., 2000; Lund and Rahbek, 2002; Danielson and Treadaway, 2004; Warman et al., 2004a). This approach is flawed because only one of a large number of alternative flexible area sets is considered in each case, which may be unrepresentative of the entire population of sets. Comparing irreplaceability scores (Warman et al., 2004b) does not solve the problem for our purposes, because irreplaceability is a measure of flexibility, which depends most strongly on the rarest species present (Pressey et al., 1994), and is not a measure of overall complementarity (Williams, 2001). A general shortcoming of the spatial overlap approach is that it says nothing about whether or not areas within the subset of overlapping areas include most of the complementarity, or make only minor contributions. It would be possible for the complementary contribution for an ‘overlap’ area to differ strongly between the predictor and predicted groups of organisms.

The third and more common approach recently has been to apply complementarity-based area selection using a surrogate and then sum up the representation of another group within the area set. This approach, although a good start, has limited value because the results include only one area set (e.g., Ryti, 1992; Dobson et al., 1997; Howard et al., 1998; Andelman and Fagan, 2000; Reyers et al., 2000; Virolainen et al., 2000; Lund and Rahbek, 2002; Beger et al., 2003; Moore et al., 2003; Warman et al., 2004a), or include all flexible sets or a large sample of flexible sets (e.g., Williams et al., 2000; Hopkinson et al., 2001; Manne and Williams, 2003), but not the overall pattern of complementarity. In order to assess the surrogates for broader biodiversity more usefully, we need methods for assessing whether they are good predictors of complementarity across all areas.

1.4. A new approach to complementarity analysis

We propose a new approach to assessing how well surrogates predict complementarity. Fig. 1 illustrates the principles. The fundamental measure is the complementary richness of a focal biota for one area with respect to a reference biota of other area(s) (which might be under some form of conservation management, referred to here for convenience as a ‘reserve’). This complementarity measure is then plotted for the surro-
gate or predictor on the \(x\) axis, against the corresponding complementarity for the same area comparison but for overall biodiversity on the \(y\) axis. The reference biota in this comparison can be contributed by any number of areas: from 0 (whereupon the calculation simplifies to one of species richness); to a single area; to a set of \(n\) areas; up to the total of all other areas with records (whereupon the calculation simplifies to one of ‘endemism’ at the scale of the analysis). For a set of \(n\) areas, there are \(n^2 - n\) area comparisons. When dealing with large numbers of grid cells, this number of comparisons becomes very large (in the British \(10 \times 10\) km grid data, more than \(5 \times 10^6\) comparisons for each of the two groups being compared). Therefore for this paper, the focal area and a single reference area are both selected at random to make a sample of comparisons (Fig. 1). The solid lines in Fig. 1 show the median scores on each axis from this sample.

A problem for analysing the pattern in Fig. 1 is the inevitable inter-dependencies among areas. This has two major components. First, there is spatial autocorrelation within species’ distribution patterns. However, this is a biologically interesting property of species’ distributions, which in our view deserves to be included in the analysis (e.g., Williams and Gaston, 1998). Second, pairwise comparisons among areas or among groups of areas for complementarity inevitably bring in dependencies among areas. Both components contravene a basic assumption required for the standard tests of correlation: that data points be independent for counting degrees of freedom. This does not affect correlation coefficients, but prevents us from applying standard statistical tests of significance.

To address the problem of inter-dependence among data points within complementarity analysis, we compare segments of the frequency distribution. We examine the numbers of points falling within the opposing upper and lower quartiles on the plot (dotted lines in Fig. 1), which correspond to false high (abbreviated here to FHI) and false low (or FLO) predictions. To test for significant predictivity of complementarity by surrogates, we then assess whether the numbers of these departures from a predictive relationship are significantly lower than expected by using a null model to reassign local biotas at random.

We also ask: what is the spatial distribution of FHI and FLO predictions? We are interested to know where in geographical space are the potential weaknesses within surrogate relationships, and how these vary among group comparisons. We are interested in this because their distribution might tell us something about the factors contributing to these weaknesses. We would like to understand those situations in which even usually good indicators of complementarity will not always work.

## 2. Methods

### 2.1. Data

Prendergast et al. (1993b) and Prendergast and Eversham (1997) chose to use the fauna of Britain to investigate surrogate relationships because the region is fortunate in having some of the best species-based distribution data of any country in the world (Anonymous, 1994; Lawton et al., 1994). These data result in major part from information collected by volunteer recorders and collated on a \(10 \times 10\) km grid by the Biological Records Centre (BRC; Harding and Sheail, 1992) and by the British Trust for Ornithology (BTO; Gibbons et al., 1993). Only the most recent date classes from each published data set are used in our analyses.
As a stand-in for overall biodiversity in our assessment, we use a large and ecologically diverse group: the vascular plants, surveyed between 1970 and 1999 (Preston et al., 2002). Species richness of plants is relatively uniform across Britain, with a weak trend to increasing richness towards the southeast. This stand-in is necessary because the whole justification for the need for surrogates is that true overall biodiversity cannot be measured directly.

As potential surrogates for use in predicting our stand-in for overall biodiversity, we have selected three groups (Table 1). The effectiveness of predictors of complementarity has been found to be strongly affected by the number of surrogate species (Manne and Williams, 2003). Therefore, each group is selected to be nearly equal in number of species, with approximately 100 species, equivalent to 7% of the number of vascular plants in Britain. Our first group is a terrestrial subgroup (doves, raptors, and passerines, from the classification of Sibley and Ahlquist, 1990) of breeding (confirmed and unconfirmed breeding records) birds, surveyed 1988–1991 (Gibbons et al., 1993). Birds have been a favourite surrogate in biodiversity studies because they are so popular and consequently well recorded. Richness in these species is particularly uniformly distributed across Britain. Our second group is a composite of two of the better-recorded insect groups: dragonflies, surveyed 1975–1990 (Merritt et al., 1996), and butterflies, surveyed 1970–1982 (Heath et al., 1984). They represent predominantly southern, warmth-loving groups of invertebrates. Our third group is a subgroup (suborder Jungermanniineae in the sense of Crandall-Stotler and Stotler, 2000) of liverworts, surveyed 1950–1989 (Hill et al., 1991). These are well-known for favouring the wetter and cooler north and west of Britain and so have a richness distribution that contrasts with many other groups of species.

### Table 1: Distribution data are published records for 10 × 10 km grid cells from some of the best-recorded British groups

<table>
<thead>
<tr>
<th>Name</th>
<th>Included groups</th>
<th>Total number of species</th>
<th>Median range size of species (number of British cells)</th>
<th>Total number of British cells with records</th>
<th>Correlation of richness with richness of vascular plants (in shared areas)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birds</td>
<td>Doves, raptors + passerines</td>
<td>105</td>
<td>1327</td>
<td>2806</td>
<td>0.57</td>
</tr>
<tr>
<td>Insects</td>
<td>Dragonflies + butterflies</td>
<td>97</td>
<td>378</td>
<td>2684</td>
<td>0.63</td>
</tr>
<tr>
<td>Liverworts</td>
<td>Jungermanniineae liverworts</td>
<td>109</td>
<td>75</td>
<td>1964</td>
<td>-0.25</td>
</tr>
<tr>
<td>Vascular plants</td>
<td>Ferns, conifers + flowering plants</td>
<td>1353</td>
<td>355</td>
<td>2798</td>
<td>1</td>
</tr>
</tbody>
</table>

All figures refer to records only from within Britain, without Northern Ireland, and to the most recent date classes in each data set. Correlation coefficients are Spearman ρ.

2.2. Analysis

We start by drawing a random sample from among all grid cells shared between groups from which to count pairwise complementarity in richness of numbers of species, as shown in Fig. 1. For example, for birds sharing 2776 grid cells with vascular plants, we take a sample of 2776 comparisons of one (focal) grid cell, chosen at random, to another (reference) cell, also chosen at random. We are also able to consider complementarity of a random sample of focal cells to reference sets of larger numbers of ‘reserve’ cells (chosen at random). In assessing the strength of the prediction shown in Fig. 1, four classes of relationship are considered (e.g., Sokal and Rohlf, 1981): true high estimates and true low estimates, together with false high (FHI) estimates and false low (FLO) estimates. We have chosen to define thresholds for ‘high’ and ‘low’ from the quartiles in the frequency distributions of scores on each axis observed in our sample. When combined between axes, these quartile thresholds describe boxes to the lower right and upper left of Fig. 1, containing the observed FHI and FLO predictions, respectively. The numbers of false predictions within these boxes can then be counted.

The strength of prediction observed is assessed against the strength expected by chance. For example, for birds sharing 2776 grid cells with vascular plants, we take the same sets of cell-pair comparisons as above (so that the test is based on the same sample of complementarity scores), but randomly re-assign the pairs of cell-pair comparisons between birds and plants, and repeat this 1000 times. From this new distribution of randomised ‘predictions’ and their counts of FHI and FLO predictions, we identify the thresholds to the lowest 5% of counts. If the values of these lowest 5% expected counts are higher than the observed counts, then the observed counts are interpreted as being significantly lower than expected by chance.

The spatial distribution of FHI and FLO predictions can be plotted for each grid cell on a map. Because complementarity can be highly asymmetrical (see Section 1.3), we could examine comparisons in either direction between pairs of cells: such as (a) the complementarity TO each cell in turn of all of the other cells; or (b) the complementarity OF each cell in turn to all of the other cells. We see the latter (OF) case as being more relevant to the situation of having to choose an area to complement other areas. This map could be helpful in addressing the question: where (for which kinds of areas) would we expect prediction of complementarity to break down?

For each cell, we measure complementarity for both the predictor and the predicted group, so there are in effect a series of plots like Fig. 1, one for each cell. For each of these single cell ‘plots’, we count the number of complementarity comparisons that fall within the FHI and FLO quartile boxes as defined by the first random sample. Using a two-colour overlay technique (Williams and Gaston, 1998), we plot the counts of FHIs and FLOs for each cell on a single map to examine the spatial pattern of the relationship between the two (relative to the national pattern). The quantitative methods used here have been implemented in the WORLDMAP software (Williams, 1999).
3. Results

3.1. Mapping complementarity

Fig. 2 shows the geographical distributions of species richness and median complementarity of each grid cell on the map to the other grid cells for the vascular plants and for each of our surrogate groups. Within each group, species richness and this measure of complementarity have high correlations (Spearman \( \rho \): birds 0.83; vascular plants 0.97; insects 0.98; liverworts 0.98). These differences among groups in \( \rho \) broadly parallel differences in median range size (Table 1), because large range size (birds) must constrain complementarity among biotas, reducing its dependence on richness. Similarly, the respective frequency distributions of richness and complementarity are similar for the insects and liverworts (histograms in Fig. 2), but for the vascular plants and more especially for the birds, complementarity tends to be skewed towards lower scores than richness.

3.2. Assessing the strength of predictions

We compare the birds, insects, and liverworts as surrogates for predicting complementarity among British vascular plants in Table 2. Two inferences are drawn for these surrogates at the scale of 10 × 10 km grid cells in Britain. First, only the first two relationships show significantly fewer FHI and FLO predictions than expected by chance. Therefore, these liverworts (non-vascular plants) perform worst among the three groups and are not considered effective predictors of complementarity among vascular plants. Second, the birds show slightly more false predictions and are therefore a poorer predictor, whereas the insects are a better predictor. These results show the same rank order of strengths as the correlations in species richness between surrogates and vascular plants in Table 1 (column 6).

3.3. Changes in predictivity as reserves are selected

We plot the changing surrogate relationships as the number of reference ‘reserves’ increases in Fig. 3. In the first plot, there are no reference cells, so the scores for each focal cell are simply the species richness scores for those cells. When there is one reference cell, then the scores for the focal cell are complementarity with respect to that single cell. As the number of reference cells (which could be the number of cells in an existing reserve network) goes up, so the score for the focal cell becomes increasingly dependent on some of the most narrowly distributed species in the data (Table 3, apparent from the declining mean range sizes in columns 2 and 3). Fig. 3 shows that as the number of reference areas increases there is an increase in the scatter of the predictive relationship, so that the strength of the predictive relationship decreases as shown by the increasing percentage of false predictions (Table 3, columns 4 and 5). However, even with
16 reference areas, the predictivity of complementarity remains significant.

3.4. Geographical distribution of false predictions

We draw four inferences from the mapped distribution of FHI (blue) and FLO (green) predictions in Britain in Fig. 4.

First, grid-cell scores are highly right skewed, with only a very few cells contributing high numbers of false predictions in either direction and most cells having very low numbers of false predictions. For example, in the lower left map of Fig. 4, almost all cells have less than 200 total FHI and FLO counts from the bird OF comparison, with just a very few cells having counts of more than 1000. Therefore major prediction failures are rare among grid cells for these data.

Second, scores in the two groups of quartile tendencies towards FHI (blue) or FLO (green) predictions are spatially dissociated rather than associated within the same cells (Table 4) and are spatially aggregated within different broad
regions of Britain. Therefore, false predictions appear to show some geographical pattern, which may be evidence of spatially differentiated governing processes. Factors affecting these processes might be sought inductively by spatial correlation.

Third, geographical patterns in false predictions are not consistent when using different predictor groups. Comparing maps along the lower row of Fig. 4, birds and liverworts show more blue FHI cells in the north and more green FLO cells in the south, whereas the opposite is shown for the insects. Therefore, factors affecting governing processes might be associated with differences in ecological characteristics among the predictor groups.

Fourth, there is a tendency to reversing the kinds of false predictions between the TO cells and OF cells in the complementarity maps (comparing maps down columns of Fig. 4), i.e., FHI predictions for complementarity in one direction (OF) correspond to FLO predictions in the other (TO) and vice versa. For example, this is shown more directly in Fig. 5 for the bird comparisons from the maps on the left of Fig. 4, in which high values on each axis always correspond to low values on the other axis. Part of the explanation for the opposing regional patterns of false predictions is likely to be that (a) complementarity OF cells tends to be associated with richness within each group of species (e.g., high complementarity scores for an area are expected to be associated with high species richness in that area, see Fig. 2, because high richness is likely to provide many additional species that can be added) and (b) there are often some regions with broadly divergent patterns of relative richness between any two groups of species (Fig. 2).

4. Discussion

4.1. Caveats

Many possible shortcomings of atlas data may have biased our results. An insidious form of bias comes from having many unsampled cells excluded from the analysis, because the excluded cells may be particularly likely to show poor correspondence between groups.

Among the most important sources of bias for studying surrogacy is co-varying sampling biases between groups, which might lead to over-estimation of the co-occurrence of groups among sites. For example, sampling may have been directed primarily to a few well-known, semi-natural sites. But biases of the opposite kind might also occur, for example if specialists in any two groups preferred to sample different kinds of habitat. They might both avoid sampling intermediate habitats, thought to be less favourable, where the groups might be more likely to co-occur. These biases, although unknown, are an unavoidable property of data in all studies of surrogacy and a property towards which the relationship will need to be relatively robust. In future studies, it would be useful to assess the robustness of surrogacy relationships by studying the effect of data degradation.

4.2. Using the maps

How can complementarity maps help in selecting areas to conserve biodiversity? As outlined in Section 1.3, between-group correlations or comparisons of simple median complementarity scores (Fig. 2) could be misleading when considering surrogacy. Our approach to mapping FHI and FLO areas overcomes these problems and provides useful new information.

Our maps in Fig. 4 show the geographical clumping of errors in the surrogacy relationship. For example, when considering particular surrogates, areas identified by high FHI predictions in Fig. 4 (blue) are over-valued by the surrogates and therefore could be an inefficient use of scarce conservation resources. In contrast, areas with high FLO predictions in Fig. 4 (green) are under-valued and if, as a consequence, they remain unprotected, they could leave important high biodiversity exposed to a risk of loss. This begs the question: are high FLO areas more attractive to damaging land uses than would be expected by chance? In future studies it would be useful to examine the distribution of these areas in relation to the intensity of threats. It would be doubly unlucky to fail to predict areas of high biodiversity where people are also particularly likely to threaten its persistence.

How should conservationists respond to these errors in a surrogacy relationship? Areas with high FHI predictions will be problematic because they could cause high conservation expenditure for society with little biodiversity gain. However, in principle this situation is reversible in that these areas could be released from conservation management in the future. There is an asymmetry in that the same reversibility does not apply to areas with high FLO predictions if they
remain unrecognized for conservation, particularly if they are highly threatened. This is the worry for any surrogacy approach, which demands a way of assessing relationships. Our method provides this. As a precaution, more effort will need to be put into re-surveying or ground-truthing a surrogacy relationship, to ensure that areas appear in the same part of the graph when re-surveyed. This will be particularly important when small surveys have been used to assess very rich areas, especially when there is a possibility of divergent habitat associations, for example between samples from road-edge surveys and the rich biotas of forest interiors (e.g., in New Guinea: Faith et al., 2001).

Fig. 4 – Geographical distribution of relative numbers of quartile false high predictions (FHI, increasing blue) and false low predictions (FLO, increasing green) of vascular plants on a 10 x 10 km grid for Britain (white shows low numbers of both, black would show high numbers of both) using an equal-interval colour scale. The predictor groups are (left) birds, (centre) insects, and (right) liverworts (see Table 1). Maps in the top row show complementarity TO each cell of all other cells, whereas maps in the lower row show complementarity OF each cell to all other cells.
4.3 Better surrogates

Why are some groups of organisms better predictors of complementarity than others? One approach to discovering which characteristics of species make them better components for more successful surrogate groups has been to study broad characteristics of the better species (Manne and Williams, 2003). Here, we take a complementary approach, examining spatial variations in predictor performance across the entire group of surrogate species, with the aim of associating high rates of false prediction with particular historical or ecological factors. At least two reasons have been proposed for shared patterns between surrogates and broader biodiversity. First is shared historical vicariance (e.g., Williams, 1996; Moritz and Faith, 1998; Williams et al., 2000). This kind of explanation is unlikely to be important within Britain, or within any other region of similar size, unless major barriers or tectonic boundaries are present (mountain ranges, plate-joining zones, etc.). Second is shared ecological complementarity (e.g., Ryti, 1992; Faith and Walker, 1996a; Williams et al., 2000). Within Britain, there are many strong and correlated environmental gradients, particularly in temperature, precipitation, and geology, between the northwest and southeast that might influence some groups of species in similar ways. For example, the insect groups we consider are well known as showing higher richness in the warmer and drier south and east, whereas the liverworts show higher richness in the cooler and wetter north and west (Fig. 2).

We should not expect to find a single explanation for differences in predictivity of complementarity, because our maps in Fig. 4 show that patterns of false prediction differ among surrogate groups. Nonetheless, group-specific factors may be identified. For example, in the OF cells comparison in Fig. 4 (lower row), the birds and liverworts on the one hand, and the insects on the other, show almost opposite patterns between northern and southern Britain. The green regions show where there is relatively more complementarity in plants than in birds and liverworts in southern Britain, but relatively more complementarity in plants than in the butterflies and dragonflies in northern Britain (all surrogate groups show consistently higher complementarity than plants in Wales). The difference between these patterns is presumably related to the greater relative diversity of birds and liverworts in northern Britain compared to most insects. In turn this is related to birds being warm blooded and with many strongly migratory species (compared to dragonflies

\begin{table}
\centering
\begin{tabular}{|c|c|c|}
\hline
 & Birds & Insects & Liverworts \\
\hline
TO cells & -0.73 & -0.56 & -0.71 \\
OF cells & -0.74 & -0.57 & -0.69 \\
\hline
\end{tabular}
\caption{Spearman correlation coefficients between numbers of quartile false high (FHI) predictions and false low (FLO) predictions of vascular plants on a $10 \times 10$ km grid for Britain from Fig. 4.}
\end{table}

The predictor groups are birds, insects, and liverworts (see Table 1). Coefficients in the top row show complementarity TO each cell of all other cells, whereas coefficients in the lower row show complementarity OF each cell to all other cells.

\begin{figure}
\centering
\includegraphics[width=\textwidth]{scatter_plots.png}
\caption{Scatter plots of numbers of quartile (a) false high (FHI) and (b) false low (FLO) predictions per British $10 \times 10$ km grid cell from Fig. 4 (upper left) birds predicting vascular plants ‘TO cells’ comparison compared to Fig. 4 (lower left) passerine birds predicting vascular plants ‘OF cells’ comparison.}
\end{figure}
and butterflies, which are both essentially cold-blooded and have some but fewer migratory species) that can persist in the north by avoiding cold winters, while liverworts need cool damp conditions to avoid desiccation. Insects are more similar to vascular plants, with greater diversity in the south, where higher temperatures, a longer growing season, and greater productivity favours greater diversity. These may be familiar patterns, but they demonstrate that our mapping technique should be capable of revealing potentially useful habitat-based limitations to other surrogacy relationships, at different spatial scales, and for different regions of the world.

These results support those of a previous quantitative analysis seeking good predictors of complementarity (Manne and Williams, 2003) in showing that a combination of properties is required. For example, Ryti (1992) and Williams et al. (2000) had suggested that an important factor for good performance is small range sizes in the predictor group. Among the predictor groups we studied (Table 1), liverworts have the narrowest range sizes, and yet they were the poorest predictors of vascular plants (Table 2). In contrast, our insect groups, which combine the next smallest range sizes (Table 1, column 4) with ecological requirements shared more closely with vascular plants (a requirement of surrogates suggested by Kremen, 1992; Faith and Walker, 1996b; Williams et al., 2000), gave the best predictions of complementarity for vascular plants (Table 2). Like Moore et al. (2003) and Lund and Rahbek (2002), we found that birds, with their large range sizes, performed less well as surrogates, despite the perception that they are a good indicator group for general biodiversity (ICBP, 1992).

4.4. Limitations to surrogates

Previous studies have reported that narrow range and threatened species are the ones most likely to be missed when using a surrogate approach (Dobson et al., 1997; Fjeldså, 2000; Reyers et al., 2000; Bonn et al., 2002; Moore et al., 2003). Moore et al. (2003) suggested that this is because there is lower congruence between groups in the distribution of rarer species than in species richness.

Our results illustrate the nature of the relationship between surrogacy and rarity. As more areas are selected and the predictivity of complementarity is re-assessed (Fig. 3), continuing good predictive performance depends on maintaining congruent patterns of distribution between the remaining complementary predictor and predicted species. In practice, the surrogacy relationship passes through two phases as the congruence breaks down. We show that, initially, there is a first phase with strong correlation for species richness (Table 1, Fig. 3(a)), so that the first area chosen will be highly predictive. We see that even after selecting the first area, selecting another complementary area results in good representation of the predicted organisms (Fig. 3(b)).

But as more areas are added to the reference set of ‘reserve’ cells, then the remaining complementary species become a residue of progressively more narrowly distributed species (Table 3, columns 2 and 3). In practice this creates a second phase, because in these data as the remaining species become rarer, their distributions become more scattered and incongruent (Fig. 3(c) and (d)), as shown by the increasing percentage of false predictions (Table 3, columns 4 and 5). Consequently, in the second phase, as more areas are selected, the predictivity of complementarity declines. This incongruence in distribution among some of the rarer species may be explained in part by differing survey biases, by metapopulation effects, or by species’ highly idiosyncratic specializations, both within and between groups. This is apparently despite the possible effect suggested by Lund and Rahbek (2002) that human management might have extirpated species from many sites, thereby artificially increasing relative co-occurrence in the remaining semi-natural sites.

4.5. Conclusion

Our results provide encouraging support for the value of the surrogacy approach in the context of selecting networks of conservation areas. This is in direct contrast to Lund and Rahbek (2002), who concluded that the surrogacy approach would be an ineffective method for the representation of overall biodiversity if only 10% of the area could be managed for conservation. The reason for the difference lies in the different methods of analysis. They examined overlaps in single sets of selected areas, finding low overlaps when few areas were selected. Our method provides a broader sample of complementarity predictions, measured more directly in terms of the numbers of species represented. We are also able to show why surrogacy often works particularly well when only a few areas are selected, because many of the species included are relatively widespread.

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