Modelling biodiversity distribution in agricultural landscapes to support ecological network planning

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Abstract

Strategic approaches to biodiversity conservation increasingly emphasise the restoration of ecological connectivity at landscape scales. However, understanding where these connecting elements should be placed in the landscape is critical if they are to provide both value for money and for biodiversity. For such planning to be effective, it is necessary to have information of the distributions of multiple taxa, however, this is of poor quality for many taxa. We show that sparse, non-systematically collected biological records can be modelled using readily available environmental variables to meaningfully predict potential biodiversity richness, including rare and threatened species, across a landscape. Using a large database of ad-hoc biological records (50 501 records of 502 species) we modelled the richness of wetland biodiversity across the Fens, a formerly extensive wetland, now agricultural landscape in eastern England. We used these models to predict those parts of the agricultural ditch network of greatest potential conservation value and compared this to current strategic network planning. Odonata distribution differed to that of other groups, indicating that single taxon groups may not be effective proxies for other priority biodiversity. Our results challenged previous assumptions that river channels should comprise the main connecting elements in the Fens region. Rather, areas of high ditch density close to a main river are likely to be of greater value and should be targeted for enhancement. This approach can be adopted elsewhere in order to improve the evidence-base for strategic networks plans, increasing their value for money.

HIGHLIGHTS

- We used ad-hoc biological data to model landscape-scale wetland species richness.
- Models were used to assess and improve a proposed ecological connectivity network.
- Our evidence-based network was shorter and connected areas of higher richness.
- Our results challenge previous assumptions of important network elements.
- Odonata were poor proxies for other groups of wetland species.

1. Introduction

Habitats are increasingly fragmented. Furthermore, in human landscapes, habitat patches are often surrounded by land uses that are potentially hostile to dispersal, increasing functional isolation (Nowicki et al., 2014). Such habitat fragmentation and isolation increase local population vulnerability to extinction and reduced dispersal opportunities limit species’ ability to respond to climate change, further reducing biodiversity resilience (Hill et al., 2002). Strategic approaches to conservation are, therefore, increasingly focused at the restoration of landscape connectivity by the creation of movement corridors, stepping stones or by improving landscape permeability (Dolman, 2012; Lawson et al., 2012; Saura et al., 2014). However, the nature, size and placement of these connecting elements are critical if investment of finite funds and land resources are to give optimal returns. There are several key issues to the success of landscape connectivity; identifying what species should be targeted within a landscape (Dolman et al., 2012), ensuring that the connectivity elements comprise habitats that suit these species and establishing where these connecting elements should be placed.

Ecological networks are often designed to enhance the metapopulation viability of individual high profile species, such as top predators (Klar et al., 2012) or other mobile species (Bani et al., 2002). However, the ability of such species to act as connectivity umbrellas for assemblages of other species may be limited (Cushman & Landguth, 2012) because the suitability of the habitat and type of connecting element differs amongst taxa. For example, while linear field margins may provide connectivity to some generalist butterflies (Delattre et al., 2010), they may act as sinks to other taxa (Krewenka et al., 2011). Similarly, hedgerows are often purported to provide suitable corridors for woodland species, but may only provide habitat for woodland edge species (Liira & Paal, 2013). The planning of landscapes to provide resilience for assemblages of regional biodiversity therefore requires the consideration of multiple relevant taxa (Zulka et al., 2014).

Decisions regarding the optimum placement of connecting elements should be made using evidence of the current and potential distribution of a full complement of target species. Existing protected sites that retain a concentration of rare species generally form the focus of connectivity networks (Beier et al., 2011) and the existence of species within these fragments is often well known. However, our understanding of the distribution of species throughout the rest of the landscape is incomplete, with some locations receiving high levels of recording effort and others very little. Poorly recorded areas that are nevertheless potentially suitable for a species may harbour unrecorded residual populations, or be more likely to be colonised if both habitat quality and connectivity are improved (Lawson et al., 2014). Unsystematically collected biological data therefore do not provide a reliable assessment of conservation value or potential across a landscape. This results in reliance on expert opinion in the design of landscape connectivity (Beier et al., 2009; Eycott et al., 2011). However, if the patchy nature of recording effort is accounted for in the analysis (Kéry, 2011), ad hoc biological data can be exploited to provide more objective design of landscape connectivity.

In this study, we use the Fens, a formerly extensive wetland system in eastern England, to demonstrate how connectivity planning can be informed by modelling ad hoc biological records with easily obtainable, landscape-scale environmental data. Remaining wetland habitat in the Fens is highly fragmented and isolated within an intensive agricultural landscape, but there is a high potential for connectivity through enhancing management of linear drainage ditches. Ditches in intense agricultural areas are often rather different to natural streams (Herzon & Helenius, 2008), supporting lower biodiversity (Williams et al., 2004); however, they can act as reservoirs for important regional wetland biodiversity (Simon & Travis, 2011). Biological recording within the wider Fens landscape is extremely sparse, so simple mapped biological richness cannot be used as an evidence base for selecting potentially biodiverse ditches for improved management or in the design of connectivity networks. Recent attempts at strategic planning (e.g. Fens for the Future Partnership, 2012) have therefore relied on a combination of expert opinion and untested assumptions of where this targeted management should be placed.

We take the approach of modelling potential biodiversity value in relation to underlying environmental factors and landscape context, to predict where in the landscape targeted management to enhance habitat quality will have greatest potential to support biodiversity and enhance connectivity. We use an extensive but unevenly distributed database of 67,395 ad hoc biological records to model the richness of groups of wetland species across the Fens landscape in relation to a range of coarse-scale environmental and landscape factors. Using these models, we aim to: 1) predict and map the potential richness of groups of wetland species in order to identify parts of the landscape of greatest potential conservation value; 2) apply these maps of predicted biodiversity potential to assess current strategic planning maps.

2. Methodology

2.1 Study area

The Fens, covering almost 4,000 km^2 of eastern England (Fig. 1), was formerly an extensive wetland area but only 1% of wetland habitat remains. This habitat is concentrated in six key protected areas, which are each small (mean area 819 ha) and isolated within the country's most important arable agricultural landscape. More than 20 million km of ditches and drainage channels criss-cross the Fens landscape and by targeting selected ditches for enhanced management, the ditch network presents an excellent opportunity for increasing both habitat area and connectivity for wetland species. However, the current conservation value of large parts of this landscape is poorly known.

2.2 Biological data

All available species observations (records) were collated for the period of 1987-2012 from the 4147 1-km squares wholly or partly within the Fens Natural Character Area boundary (Natural England, 2013), with an extension (3 km from the boundary) to include Chippenham Fen, one of the three important relict fen sites in the Fens. Records were compiled from Local Biological Records Centres, the National Biodiversity Network (NBN) gateway, national and county natural history and recording societies whose records were not available via NBN, and unpublished documents or reports. Records sent to Biological Records Centres and societies are validated by expert county recorders. Although NBN data may include some unvalidated records submitted by the public, our collated species lists were validated by a range of local taxonomic experts. Records were managed using RECORDER 6 software (Joint Committee for Nature Conservation, Peterborough, UK). The study period (1987-2012 inclusive) was selected as a compromise between reflecting the current or recent distribution of wetland species and including sufficient records in the dataset to capture rare species and the potential distribution of sparsely recorded taxonomic groups. There may have been local extinctions since 1987 due to local changes in habitat quality, nevertheless the landscape predictors we consider will indicate the biodiversity potential should habitat and connectivity be restored. The majority (74%) of records were resolved to a spatial resolution of 1 km or finer and these were aggregated and analysed at the scale of 1-km grid cells. Tetrad records were assigned to all of the four 1-km squares comprising the tetrad; species records at coarser spatial resolutions were excluded. A small number of records of taxa not recorded to species level were removed. Records of marine species were excluded, but those tolerant of brackish conditions were retained. Following additional filters described below (e.g. removal of coastal squares), a database of 255 291 records remained, of which 50 501 were records of wetland plants (including conservation priority species) and conservation priority wetland invertebrates. Conservation priority species were recognised as those designated as UK Biodiversity Action Plan, Global and UK Red Data Book (except Least Concern), Nationally Rare, Nationally Scarce or Nationally Notable A and B, according to JNCC (2012), plus undesignated species with >25% of their UK distribution occurring in the Fens region – hereafter referred to as 'Fens Specialists'.

The richness of groups of wetland species were used as the biological response variables. Seven widely recorded groups of wetland species were selected for modelling that were considered good indicators of ditch quality: all Odonata (dragonflies and damselflies, 28 species), wetland plants (212 taxa), fully aquatic plants (137 taxa) and conservation priority species (including plants and invertebrates) dependent on aquatic (fully aquatic and submerged aquatic habitats, 90 species), littoral (aquatic margins, 109 species) or wetland (208 species) habitats, and Fen Specialists (58 species). Wetland plant species were defined as all Characeae (stoneworts, multi-cellular branched macro-algae) and those vascular plant species associated with freshwater (aquatic, wetland or seasonally wet) habitats selected from Hill et al. (2004) with Ellenberg moisture values ≥7 (species with Ellenberg salinity values of >5 were excluded). Aquatic plants were a sub-set of the wetland plants, classified with reference to existing lists by Palmer et al. (2013) and Mountford and Arnold (2006). The autoecological requirements of conservation priority species and their association with wetland, aquatic and littoral habitats, were classified following Mossman et al. (2012) and Dolman et al. (2012).

2.3 Environmental predictors

The aim of this analysis was to predict the distribution of wetland species across the drainage ditch network of the arable landscape based on readily-available, coarse-scale environmental variables. Wetland Sites of Special Scientific Interest (SSSIs) were considered to be reservoirs and potential sources of high quality biodiversity, therefore 1-km squares including any part of a wetland SSSI were excluded from modelling. Wetland SSSIs were identified based on the SSSI citation description (available at www.sssi.naturalengland.org.uk), with wetland habitats considered to include ponds, gravel pits, wet woodland or carr, fen, bog, grazing marsh and wet common.

Seventeen environmental predictors were initially selected as candidates for modelling (Table 1) based on ready availability across the study landscape and considered, *a priori*, to potentially influence ditch biodiversity. A single value of each variable was calculated for each 1 km square. The mean elevation above sea level, presence of an A or B road and the distance from the centre of each 1-km square to the nearest wetland SSSI, Fenland island and the edge of the Fen basin were calculated. Previous work has suggested that ditches with highest conservation value are located near to the edge of the Fen basin or close to Fen islands (Mountford & Arnold, 2006); the reasons for this are unclear, but may relate to high water quality. Fen islands were delimited as areas of >0.1 km² with an elevation of ≥ 5 m, and the Fen basin defined as the 5 m contour boundary.

The soils of the Fens area are dominated by silt and peaty soil types. The percentages of each 1-km square comprising silt and selected peat soil types (Table 1) were calculated. Ditch isolation from main channels and from tidal influence were considered potentially important determinants of water quality, saline influence and thus of biodiversity richness. We calculated the shortest network distance along the ditches and rivers network (extracted from the Ordnance Survey (OS) surface water polylines, converted into a raster of 35m cells), from the centre of each 1-km square to the nearest main channel/river and to the tidal boundary, calculated in ArcGIS Spatial Analyst tools. Network distances were not weighted by ditch size or type, such that all cells were assigned a value of 1. A cell size of 35 m was sufficient to connect any small breaks in the polylines due to mapping error or underground drains, but was considered small enough to prevent falsely connecting ditches in close proximity that are not connected through surface water drainage. Some manual connections were imposed on the network due to large breaks in the mapped surface, for example due to bridges or pumping stations. Ditch density in each 1-km was calculated from OS polylines, which defines both banks of ditches wider than 2 m; since ditches of <2 m in width are only defined with one polyline, ditch density is an index that reflect both linear length and ditch area.

The grades of the Agriculture Land Classification were used as proxies for potential agricultural productivity, land-use intensity and therefore quality of both water and banksides; this is an ordinal scale (1-5) where grade 1 is best agricultural land. The combined percentage cover of grades 3 and 4, comprising the lowest quality agricultural land and therefore representing the lowest intensity of agricultural land-use (no land was classified as grade 5 in our study region), was used as a candidate predictor. The dominant land use in the Fens region is arable; the percentage of each 1-km square comprising un-intensively managed grassland (defined from Land Cover Map (Morton et al., 2011)) classes of Rough/Neutral Grassland) was therefore considered of interest. The percentage of urban land use was also calculated from OS data.

Inter-correlation among predictor variables was investigated using Pearson's correlation coefficient and considered large enough to potentially have an effect on the models if $r > 0.5$, following Freckleton (2002). Distance to the Fen basin was strongly correlated with distance to the nearest wetland SSSI ($r=0.533$), network distance to the tidal boundary ($r=-0.523$) and percentage of silt soils ($r=0.536$). Distance to the Fen basin was therefore excluded from the modelling, whilst the other variables were retained.

Due to comprehensive county flora, plant species recording effort was substantially greater in Norfolk and Suffolk relative to other counties. Therefore, to avoid spurious identification of any environmental factor that differed between these and other counties, when modelling the response of wetland and aquatic plant variables to environmental and landscape context indicators, we included the two county groups as a binary covariate (0 = no flora, 1 = flora).

A number of 1-km squares were excluded from the models because they contained no surface water, the surface water was more than 70 m from the nearest surface water feature (thus indicating the feature was likely to be a pond rather than a ditch, contained part of a wetland SSSI, or comprised >50% coastal area (defined using the Wash SSSI). This resulted in 3,745 1-km squares being used in analyses.

2.4 Model construction

2.4.1 Accounting for recording effort

It is well known that not all species present at a site will be detected and that this poses challenges for analysis (Chen et al., 2013), as species richness is underestimated and coefficients with environmental variables are closer to zero. Spatial variation in recorder effort can have severe consequences for models, as environmental variables that are correlated with recording effort may be spuriously identified as being related to species richness. Hierarchical occupancy modelling can address these problems by utilising repeated visits to the same site to estimate detection probabilities (MacKenzie & Kendall, 2002) and thus has applications for analysing citizen science data (Isaac et al., 2014). Despite extensions to deal with multiple species (Dorazio & Royle, 2005), application to datasets such as ours is challenged by, for example, uncertainty in defining what represents a discrete 'visit', and absence of information on visits that did not contribute species records to the data. An alternative approach to addressing spatial variation in recorder effort is to include a proxy for recorder effort as a covariate (Hill, 2011), allowing the conditional effects of environmental variables on species richness to be assessed while controlling for recorder effort. We use the total number of records in a 1-km square (i.e. including non-wetland species) as a proxy for recording effort. We expect this relationship to be saturating as species accumulation curves tend to saturate at high numbers of species, so we explored models using either square root number of records or a polynomial term for number of records, using the former as it explained more deviance. Although our method accounts for spatial variation in recorder effort, we are unable to estimate the probability of *not* detecting a species, so our estimates of species richness should be taken as an index of relative richness.

2.4.2 Predicting species richness

Statistical analyses were performed using the computing environment R (R Core Team, 2012). Predictor variables were standardised prior to modelling, with the exception of the number of records. For each response variable, we fitted generalised linear models, with a quasi-poisson error structure to deal with over-dispersion, containing all 16 predictor variables (17 for wetland and aquatic plants owing to the inclusion of county). The full model was simplified by backward elimination, judging variable retention by the t-test of β estimates, with a threshold of $\alpha<0.05$. The resulting minimum models were used to predict the richness of each of the seven wetland species groups in each 1-km square of the study area, with recording effort standardised as the overall median (41 records per 1-km square). For the wetland and aquatic plant response variables, we standardised for the presence of a recent flora by setting the value for all squares as 1.

Following Legendre and Legendre (2012), we used variance partitioning to calculate the proportion of total variation in species richness explained by recording effort (total number of records) and by environmental variables. To do this, we constructed models including 1) only environmental conditions, 2) only recording effort and 3) both environmental conditions and recording effort.

2.5 Comparison of predicted biodiversity richness to the current strategic planning maps

The 1-km squares were ranked by the predicted species richness for each of the seven biological response variables separately, where a high rank (low number) was given to squares with high predicted biodiversity. The mean of these ranks was calculated and mapped. The resulting map of predicted biodiversity was compared to the Fens for the Future

Partnership (FFFP) (2012) strategic connectivity plan. The strategic connectivity network consisted of three types of corridors: primary, secondary and landscape (Fens for the Future Partnership, 2012). The primary corridor was the priority corridor and aimed to connect three core areas thought to have high biodiversity value, the southern Fens and Ouse Washes, Holme and Woodwalton fens (and associated Great Fens Project restoration area of the Wildlife Trusts), and the Nene Washes. Secondary and landscape corridors aimed to provide additional landscape connectivity; for the purposes of this study, secondary and landscape corridors were combined.

We designed a new connectivity network that met with the objectives of the strategic connectivity network and the following criteria. Corridors must connect areas of known high biodiversity richness (wetland SSSIs) and presumed high richness, defined as those wetland Local Wildlife Sites (LWS) that were ≥0.25 km^2 and occurred in areas of high predicted biodiversity (richest ≥50% of 1-km squares). A single primary corridor was placed to connect the three core sites identified by the FFFP (2012). All corridors must join to form a continuous network across the region and, where possible, achieve such connectivity by passing through areas of greater predicted biodiversity.

The potential conservation effectiveness of the original strategic plan was compared to that of the corridor network we proposed on the basis of the predicted distribution of wetland biodiversity richness. These were assessed for each corridor strata (primary, secondary) in terms of the length within each quartile of predicted species richness (for each 1-km square, the mean of ranked richness across all the seven species groups). Proposed networks were deemed to be more effective if a greater proportion of the corridors lay within the quartiles predicted to the be most species-rich.

3. Results

3.1 Effect of the environment on wetland biodiversity richness

Overall, the minimum models explained 27.2 – 63.9% (mean = 40.3%) of the variation in species richness of the seven groups (Table 2), performing best in predicting the richness of wetland plants and aquatic plants (63.9% and 59.8%, respectively). A substantial part of the explained variance was attributed to the independent effect of recorder effort (27.3 – 76.2%). However, 17.1 – 52.8% of explained variance was attributed to the independent effect of environmental variables, and a further 2.5-26.4 % to the joint effect of recorder effort and environmental variables (Table 2). Species groups with the highest proportion of variance explained by the environmental variables were Odonata, aquatic species and littoral species (53%, 36% and 33% respectively).

The effects of many environmental predictors were consistent among species groups. Mean elevation above sea level and percentage of urban area were not significant predictors of the richness of any group (Fig. 2). A greater percentage of silt soil was negatively related to species richness of all groups, compared to all types of peat soil (Fig. 2), although the richness of wetland and littoral species were also lower with a greater percentage of deep sand over peat or peat (Fig. 2).

Richness of all groups, except Fen Specialists, was greater closer to existing wetland SSSIs. The richness of all groups except wetland plants, increased significantly with increasing values of the index of ditch density (Fig. 2). The percentage of grade 3 and 4 agricultural land (i.e. lower land-use intensity) was positively related to richness of Odonata, but not significantly related to the richness of other groups. The richness of Odonata also increased further from the tidal boundary; in contrast, the richness of aquatic species, and wetland and aquatic plants was higher closer to the tidal boundary. The distance to a main river was not significantly related to the richness of Fen Specialists and littoral species. Richness of the remaining groups was highest closer to a main river, although predicted richness generally decreased when main rivers were located on silt soils or were further from a wetland SSSI (Fig. 3). The predicted richness of all groups was low around the coast (Fig. 3).

3.2 Biodiversity potential of the proposed network corridors

The combined predicted richness of ditch species suggests that the corridors of the proposed strategic network are generally well placed (Fig. 4, 5). However, comparison of the strategic map and the predicted biodiversity richness indicated that proposed corridors do pass through some areas of lower biodiversity potential (Fig. 4). In contrast, our suggested map achieved a greater proportion of connectivity in areas of high predicted richness (88% of our corridors were located in the richest 50% of squares, compared to 66% of the FFTF corridors) for a shorter overall length (27% shorter, combined primary and secondary corridors) (Fig. 5).

4. Discussion

Landscape connectivity and conservation plans are often developed with a reliance on environmental and land cover data (Brooks et al., 2004a), but such broad data can be poor surrogates for biodiversity (Araujo et al., 2001; Schindler et al., 2013), particularly for rare or specialist species (Lombard et al., 2003). Ecological planning should consider the identity, distribution and requirements of target species in that region, rather than being based on untested assumptions of where species occur (Brooks et al., 2004b) as such assumptions can lead to inappropriate selection of habitat type or placement of the connecting elements. For example, the previous landscape connectivity plan in the Fens that was based on expert opinion selected the main river channels as a key connecting component (FFTP 2012). Whilst we found that species richness was higher closer to main river channels, rivers flowing through areas of silt soils had particularly low predicted species richness, so improvements to management or connectivity in these areas may have limited benefits for wetland biodiversity. This has important implications for other landscapes where aa single land cover variable has been the focus of network planning, because without validating with biological data the use of single features can prevent selection of optimal connectivity.

Increasing ditch density was a significant predictor of species richness for all groups, except wetland plants. The ditch density was a particularly strong predictor of priority species (those with a conservation designation) associated with littoral margins. Littoral species are of particular conservation importance in the Fens region, but are often overlooked by conservation interventions compared to submerged aquatic species (Mossman et al. 2012). Thus specifically targeting areas of high ditch density close to rivers for improved management, rather than the main river channels themselves, would substantially add conservation value. This highlights the importance of considering the identity and requirements of the species that are the priorities for conservation and connectivity in a region or a landscape.

Several broad and readily available landscape variables, such as distance to a protected site (SSSI) and cover of silt soils, were important predictors of biodiversity. Thus, such variables can be used to select areas for restoration or connectivity. The consistent negative response of species richness to silt soils may be related to reduced water quality, since sediment nutrient concentrations are higher in finer particle soils (Ockenden et al., 2012), or may reflect the contrasting deposition and landuse histories, with peat soils indicating the historic extent of freshwater marshes and earlier reclamation compared to the marine or riverine deposition of silts that were reclaimed for agriculture more recently. Previous studies have found peat substrates to have distinct flora (Mountford & Arnold, 2006) and support rare invertebrate species (Foster et al., 1989); the richness of species groups in this study were not strongly corrleated with peat substrates.

Environmental factors, such as water quality (Twisk et al., 2000) and flow rate (Leslie et al., 2012), and ditch management type and frequency (Milsom et al., 2004), are known to be important determinants of ditch biodiversity. The inclusion of such variables would certainly improve the predictive power of our models. However, such data were not available at suitable resolution across our study area, and the case is likely to be the same in other regions. We suggest that our predictive modelling approach is used in other regions to predict areas of high potential biodiversity value. Following this, the collation or collection of detailed environmental or habitat data may assist the selection of specific sites for management interventions (such as dredging and cutting), within those areas highlighted by the predictive mapping.

The effects of many environmental predictors were remarkably consistent among species groups. For example, the richness of all groups was significantly greater closer to existing wetland SSSIs. This may be because the high quality SSSI sites have acted as reservoirs of wetland species, although there may be other conditions not included in this study (e.g. water quality) that are also correlated with the distance to the SSSIs. Whilst the responses of most groups were consistent, the richness of Odonata increased further from the tidal boundary; in contrast, the richness of aquatic species, and wetland and aquatic plants was higher closer to the tidal boundary. This is an important contrast, such that network planning must either take a mixed approach, or select to prioritise either Odonata or remaining groups. Similarly, the value of wooded connectivity networks is rather different for birds, bats and beetles (Boughey et al., 2011; Davies & Pullin, 2007). This adds to previously stated concerns over the use of single taxonomic groups as proxies for other biodiversity (Noss, 1990). Recent work has demonstrated that the addition of habitat characteristics to multi-taxa proxy groups substantially improves the performance of biodiversity surrogates in spatial planning (Di Minin & Moilanen, 2014).

Biological records can be modelled with environmental variables to predict biodiversity richness across landscapes and such models have been widely used to link species distributions from atlas data to land cover data (e.g. Atauri & de Lucio, 2001; Virkkala et al., 2005). Their use here to model species richness of priority biodiversity across multiple taxa in the Fens allowed previously held assumptions about the importance of landscape features to be tested. However, the use of such methods has been limited by the lack of detailed atlas data for many taxa in many regions, with data for rare and threatened species and for poorly recorded taxonomic groups (i.e. other than vascular plants, butterflies and odonatan) particularly limited. We show that this problem can be overcome by modelling groups of priority taxa with shared ecological requirements, which allowed us to include species that would be too rare and/or sparsely recorded to model individually. This addresses a significant gap in previous large-scale studies that have omitted due to insufficient data, the rare species that are intended to benefit from the conservation measures. Our approach could be applied to any region or landscape where there has been widespread, albeit patchy biological recording.

We were then able to predict potential species richness, including multi-taxa groups of priority species, at a landscape scale and used the model predictions to make an evidence-based landscape connectivity plan, an improvement on previous plans based on untested expert judgement. Our models predict areas that have the potential for high biodiversity richness, based on their soil and other landscape variables, and we have linked these together with our proposed corridors. However, we do not know if the cells of our predicted corridor currently realise that biodiversity potential with their existing habitat, which could still be improved through enlargement or management, *or* if they currently have low habitat suitability despite high potential on the basis their landscape variables. However, in either case, we predict the potential to enhance biodiversity value and connectivity of those areas to be greater than in areas with lower intrinsic potential and thus we are recommending these areas should be targeted for enhancement.

The previous attempt to map a strategic connectivity network in the Fens (FFTP 2012) largely concurred with areas of high predicted biodiversity richness. However, our evidence-based map connected a greater proportion of areas with higher potential for biodiversity richness (22% more of our corridors were located in areas of the highest potential richness) and for a shorter overall length. Targeting areas of higher potential richness over a shorter connectivity length is more cost-effective, allowing remaining funding to be targeted to habitat management, a key influence on ditch biodiversity (Milsom et al., 2004). For example, our evidence-based predictive map provides confidence in the strategic targeting of agri-environmental measures and other means to enhance ditch management to those areas of the wider agricultural landscape that have greatest biodiversity potential for aquatic and wetland species.

Evidence-based predictive models, such as those in this study, could also be further developed to inform optimal connectivity plans. For example, predicted potential species richness can be used as a cost surface for circuit theory and other graph theory based models (Galpern et al., 2011; Rayfield et al., 2011). Although we note that the practical realization of any connectivity plan (subjective or objective) will be dependent on opportunity, landowner and other stakeholder interest, and cost (Bergsten and Zetterberg, 2013), it is crucially important to start negotiations based on evidence. Our methodology utilises ad-hoc records, and thus could be applied in any landscape or region where biological records are available, to provide an evidence-base for network planning, including rare species for which conservation actions are most needed.

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TABLE LEGENDS

Table 1. Definition and data source of environmental predictors used to model the distribution of Fens biodiversity.

Table 2. Variation in the richness of wetland groups of species explained by the minimum models.

Table 1. Definition and data source of environmental predictors used to model the distribution of Fens biodiversity.

Environmental predictor	**Abbreviation used in Figure 2**	**Source**
Mean elevation above sea level: mean elevation of all 50 m x 50 m cells within the 1 km square	Elevation	Edina Digimap Ordinance Survey (OS) PANORAMA DTM (Digital Terrain Model) 1:50,000, 50m cells
Distance to nearest fenland island: Fenland island defined as areas >0.1 km^2 with an elevation of $\geq$ 5 m (excluding coastal cliffs at Skegness and islands within large urban areas). Several large 'islands' within 1000 m of the fenland basin were incorporated into the basin, i.e. not considered islands.	Distance to Fen Island	
Distance to fenland basin: basin was defined as the 5 m contour boundary, unless the area had been defined as a fenland island.		
Presence of either an A or B road within a square	Presence of a road	OS Meridian 2 (1:50 000)
Distance to nearest SSSI comprising wetland habitats	Distance to wetland SSSI	Natural England GIS Digital Boundary Datasets
Percentage of square comprising urban areas. Urban defined from OS Strategic 1:250,000	% urban	Edina Digimap Ordinance Survey Strategic 1:250,000 VectorMap District (1:25,000)
Network distance along 'ditches' to the nearest 'main river'/coastline: calculated using network cost distance. Ditch was defined using the VectorMap District *Surface_Water* polyline for accurate mapping of small ditches and open water, and the *Tidal_Boundary* (High/Low Water Mark) polyline because the surface water data stop at the tidal boundary.	Distance to river	

Network distance along ditch/river to the tidal boundary: calculated using network cost distance (see below for full description). Ditch/river defined using the Edina Digimap *River_polyline* and VectorMap District *Surface_Water* polyline. Tidal boundary was defined as the high water mark using the VectorMap District *Tidal_Boundary* polyline.	Distance to tidal boundary	
Index length of all ditches per 1 km square: ditches were defined as above. This is considered an index because polylines defined each bank of wide ditches or rivers, resulting in double-counting, as such the lengths are not accurate.	Length of surface water	
Percentage of rough and neutral grassland	% rough/neutral grassland	Land Cover Map 2007. Centre for Ecology and Hydrology
Percentage of grades of Agricultural Land Classification: summed percentage area of grades 3 and 4	% grades 3 & 4	Natural England GIS Digital Boundary Datasets
Percentage of each peat soil type defined using Cranfield Soil Class; Peat; Seasonally wet deep peat to loam; Seasonally wet deep clay over peat (marine alluvium and fen peat) and Seasonally wet deep sand over peat (glaciofluvial drift and peat).	% peat; % peaty loam; % deep sand over peat; % deep clay over peat	NATMAP Cranfield University
Percentage of silt soil, defined as the Cranfield Soil Class “Seasonally wet deep silty”	% silt	
Occurrence of a county flora: 0/1 if in a flora recorded county	County flora	

Table 2. Variation in species richness explained by the minimum models.

	Total r^2	% variation of total r^2 explained		
		Independent effect of recording effort	Independent effect of environment	Joint effect of recording and environment
Odonata	30.4	27.3	52.8	20.0
Fen Specialists	27.2	46.4	27.1	26.4
Aquatic species	30.5	49.2	35.5	15.3
Aquatic plants	59.8	75.4	19.9	4.8
Littoral species	31.5	64.4	33.1	2.5
Wetland species	39.0	57.8	25.5	16.7
Wetland plants	63.9	76.2	17.1	6.7

LIST OF FIGURES

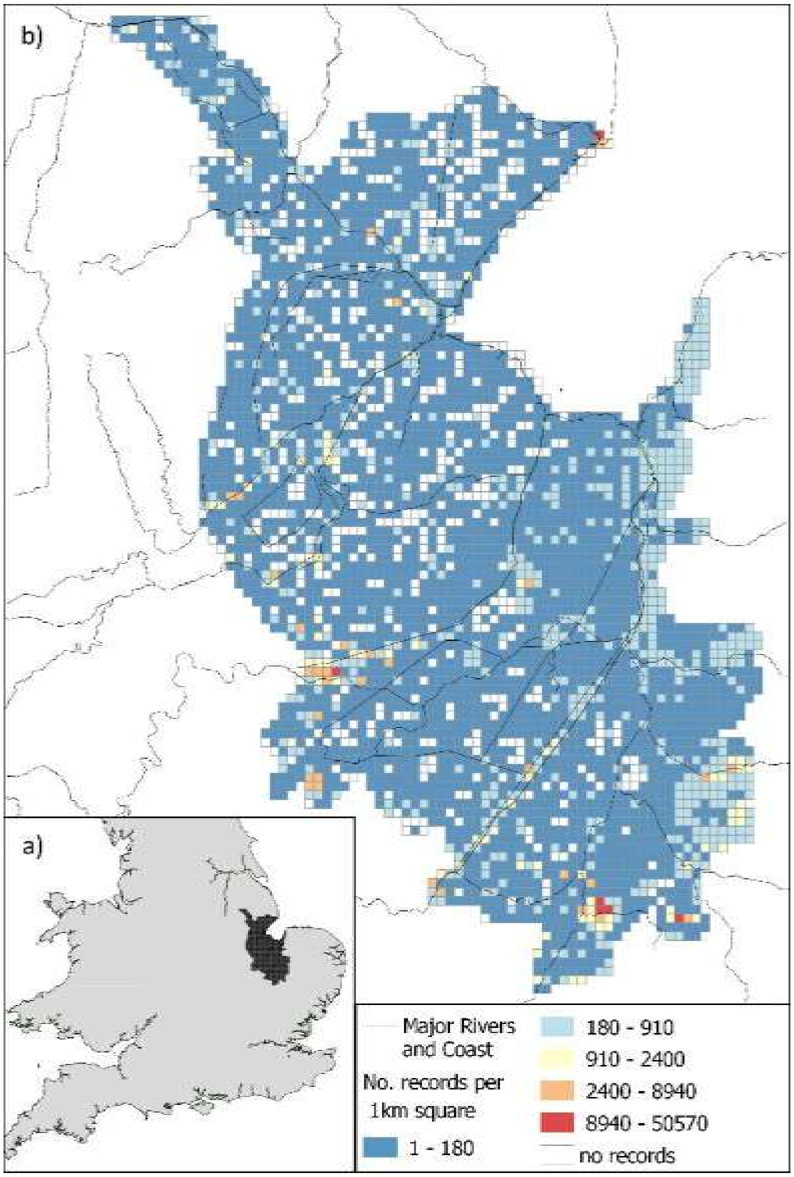

Figure 1. (a) The location of the Fens region within the UK, and b) the intensity of recording effort within the Fens, shown as number of records per 1-km square. Class intervals calculated using jenks natural breaks.

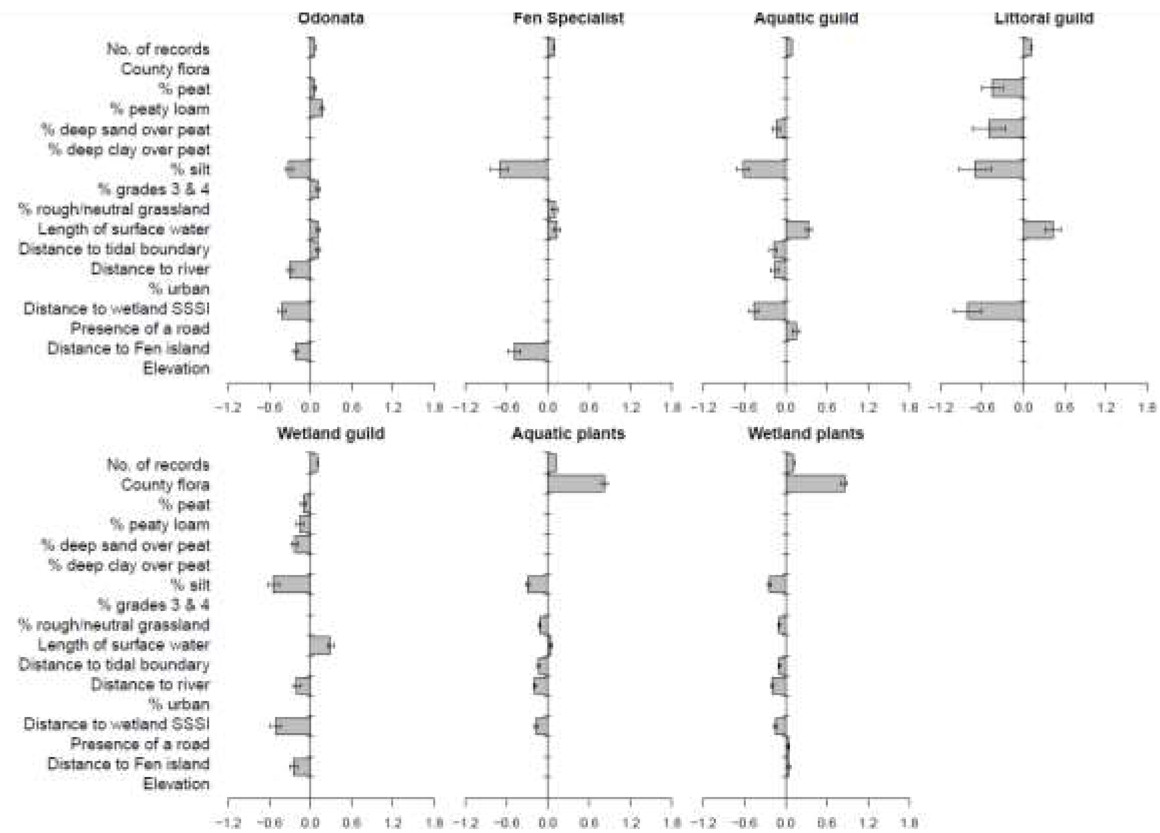

Figure 2. Mean (±SE) standardised effect size (β values) of environmental predictor variables on the richness of ditch indicator groups. Only significant ($p<0.05$) effects are shown. Predictor abbreviations are provided in Table 1.

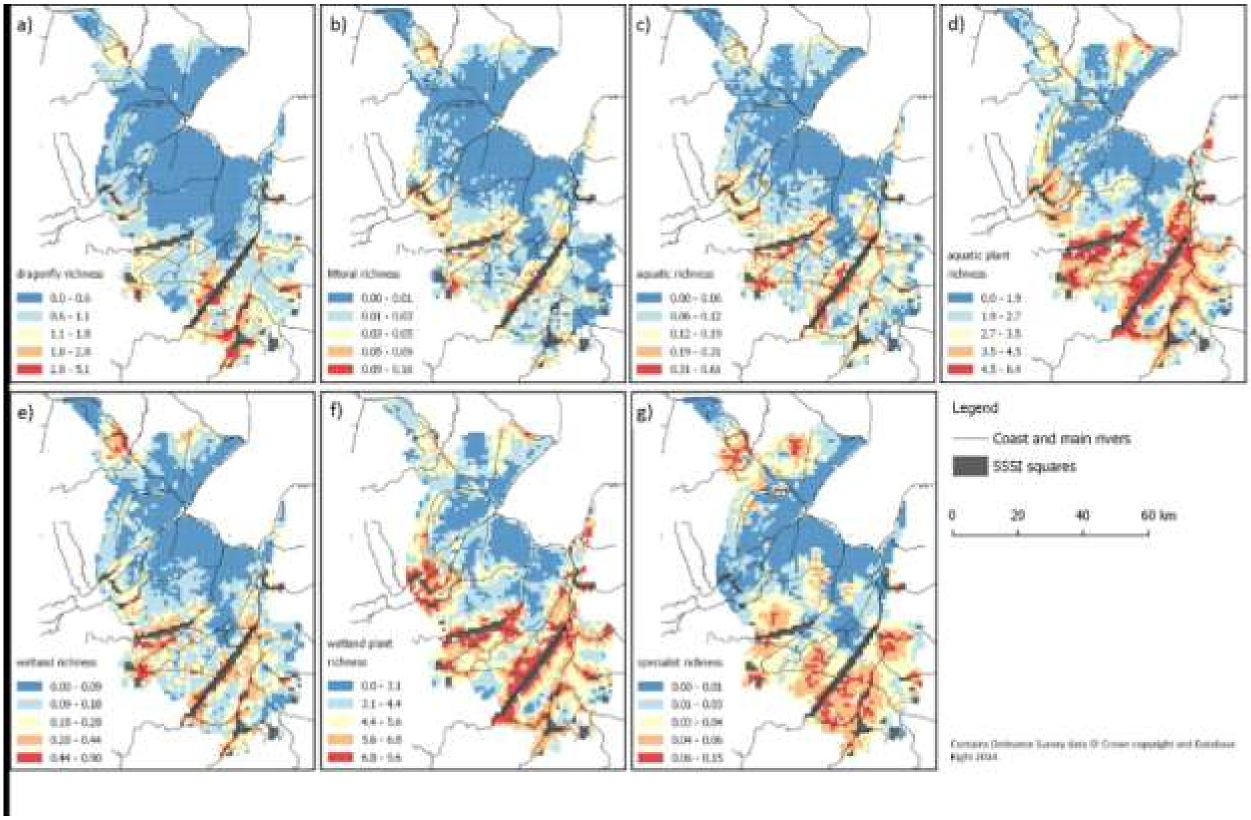

Figure 3. Predicted richness per 1-km square for a) Odonata species, b) littoral priority species, c) aquatic priority species, d) aquatic plants, e) wetland priority species, f) wetland plants, and g) Fens Specialists. White areas denote 1 km squares that were excluded from models. Class intervals calculated using jenks natural breaks.

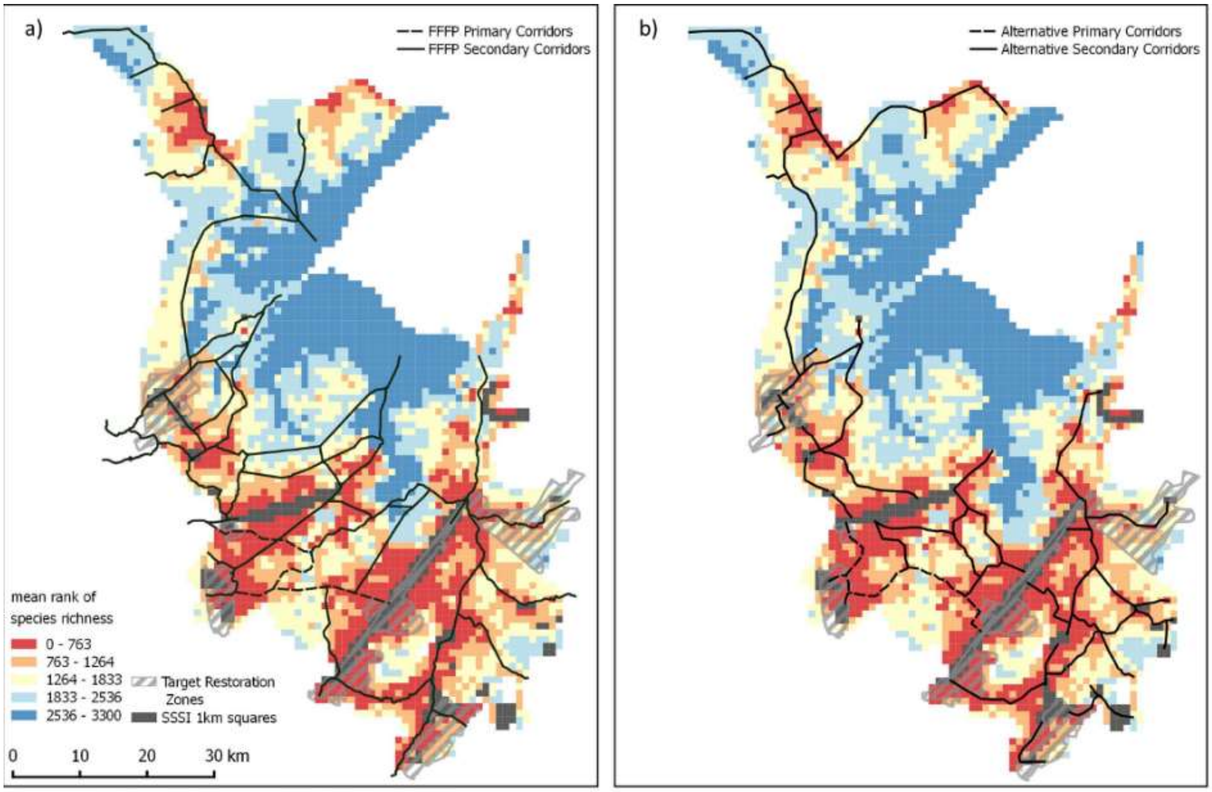

Figure 4a. Mean of the ranks of predicted species richness per 1 km square of the seven wetland biological indicator groups. A low rank (high number) is given to squares with low predicted biodiversity and high rank (tied, highest = 44) to areas with high biodiversity. Main rivers and (a) connectivity corridors proposed by the Fens for the Future Partnership (excluding the Landscape Corridor) (FFFP 2012), and (b) connectivity corridors re-routed through areas of higher wetland species richness are shown. White areas denote 1 km squares excluded from models. Class intervals calculated using jenks natural breaks.

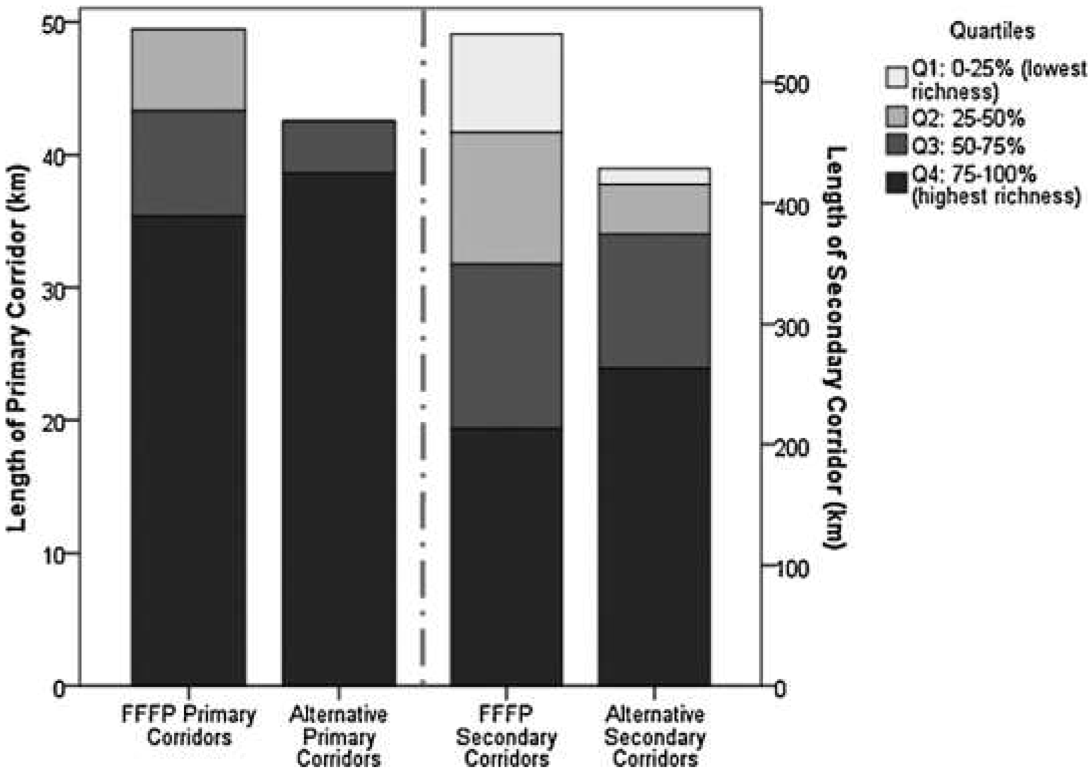

Figure 5. Length (km) of primary and secondary connectivity corridors originally proposed by the Fens for the Future Partnership and alternative corridors selectively routed through areas of predicted higher wetland richness. Bars are shaded according to quartiles of the mean of ranks of biodiversity richness per 1-km square across seven indicator groups (Q1: 44-950, Q2: 951-1561, Q3: 1562-2372, Q4: 2373-3000).