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An empirical, cross-taxon evaluation of landscape-scale connectivity

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Abstract

Connectivity is vital for the maintenance of spatially structured ecosystems, but is threatened by anthropogenic processes that degrade habitat networks. Thus, connectivity enhancement has become a conservation priority, with resources dedicated to enhancing habitat networks. However, much effort may be wasted on ineffective management, as conservation theory and practice can be poorly linked. Here we evaluate the success of landscape management designed to restore connectivity in the Humberhead wetlands (UK). Hybrid pattern-process models were created for six species, representing key taxa in the wetland ecosystem. Habitat suitability models were used to provide the spatial context for individual-based models that predicted metapopulation dynamics, including functional connectivity. To create models representing post-management conditions, landscape structure was modified to represent local improvements in habitat quality achieved through management. Models indicate that management had limited success in enhancing connectivity. Interventions have buffered existing connectivity in several species' habitat networks, with inter-patch movement increasing for modelled species by up to 22% (for water vole, *Arvicola amphibius*), but have not reconnected isolated habitat fragments. Field surveys provided provisional support for the accuracy of baseline models, but could not identify predicted benefits from management interventions, likely due to time-lags following these interventions. Despite lacking clear empirical support as yet, models suggest the management of the Humberhead wetlands has successfully enhanced the landscape-scale ecological network, achieving management targets. However we identify key limitations to this success and provide specific recommendations for improvement of future landscape-scale management. Our developments in model application and integration can be developed further and be usefully applied to studies of species and/or community dynamics in a range of contexts.

Keywords Connectivity · Landscape-scale management · Individual-based model · Hybrid model · Conservation evaluation

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Introduction

Connectivity of fragmented landscapes is considered to be of vital importance in maintaining long-term population viability in heterogeneous landscapes (Vasudev et al. 2015). Increasing attention has been given to landscape connectivity in the context of anthropogenic land-use change (Watling and Donnelly 2006) and synergistic processes such as human-driven climate change (Hodgson et al. 2011). As landscape structure is degraded and fragmented by anthropogenic modification, it is expected that this will fundamentally degrade ecosystem processes (Lawson et al. 2010). As such the creation and maintenance of functional linkages between remnant populations is essential for the long-term preservation of ecosystems in human-dominated landscapes (Benz et al. 2016).

In order to ameliorate anthropogenic landscape fragmentation, connectivity enhancement has become a conservation priority, with many resources dedicated to reconnecting habitat fragments in human-modified landscapes. However, as with many areas of applied conservation, there is concern that much of this effort is wasted on poorly planned or implemented management that often fails to enhance functional linkages between habitat islands effectively (Sutherland et al. 2004). This uncertainty about success arises from the complexities of measuring habitat connectivity in the field and in predicting the potential impacts of interventions at the landscape scale (Luque et al. 2012).

A stated aim of UK conservation policy is to produce a landscape that consists of habitats that are bigger (larger extent), better (higher quality), more (greater number), and more joined-up (enhanced ecological connectivity) (Lawton 2010). However, effective planning and evaluation of management to achieve these aims require considerable resources that are often not available. It is essential, therefore, to apply methods that make optimal use of existing data in order to determine the potential value of management options. Hybrid models are one approach that integrates different ecological processes in order to provide realistic solutions to complex problems by combining ecological principles with available ecological data. For example, habitat suitability models, that identify fragmented habitat networks based on the observed presence of a species (Merow et al. 2013), can be combined with dispersal models created either through movement rules that are already known about a given species or general ecological theory (Simpkins et al. 2018) and metapopulation models that are parameterised using known population dynamic parameters (MacPherson and Bright 2011). The strength of the hybrid modelling approach is that it enables the nested interactions between these sub-models to be represented, approaching a degree of ecological realism not possible when the sub-models are viewed in isolation (Parrott 2011).

Freshwater habitats are a particular focus for connectivity enhancement as they suffer from extreme levels of fragmentation, pollution and degradation compared to other habitats (Vörösmarty et al. 2010). River habitats represent dendritic networks along which organisms can move, but movement between network branches varies greatly between taxa (e.g. Chaput-Bardy et al. 2008). Meanwhile standing waters such as ponds and lakes are inherently isolated (Eros et al. 2012), resulting in communities structured strongly by dispersal into landscape-scale metacommunities (Heino et al. 2015). The importance of movement between water bodies as a driver of metapopulation or metacommunity dynamics has led to recognition of the importance of landscape structure between suitable habitat patches, mostly in relation to amphibians (Crawford and Semlitsch 2007). Attempts to enhance landscape-scale connectivity have focused on within-channel enhancements through dam removal (Carvajal-Quintero et al. 2017) or increasing the number of standing water bodies to improve connectivity (Williams et al. 2008).

In this study we aimed to evaluate a conservation management program that was implemented to enhance ecological connections between freshwater habitats in the Humberhead wetlands landscape in the north of England (HLP 2015). We expected that structural changes in the landscape brought about by management action would enhance functional connectivity to some degree, but that this response would be complex and vary between species depending on their habitat requirements and life history traits. In order to test this, hybrid pattern-process models were created for six putative indicator species representing the wetland community of the area. For each species, outputs from a baseline model were compared with those from a management model, in which the structural changes to habitat brought about by management interventions were reflected. By comparing baseline with management outputs we were able to predict complex population responses to structural modification that are initially unclear and difficult to detect directly in the field.

Materials and methods

Study area

As part of the response to the Lawton Review (Lawton 2010), 12 Nature Improvement Areas (NIAs) were created across the UK in 2012, of which the Humberhead Levels (HHL) NIA was one. The HHL NIA covers a 49,000 ha area and includes a variety of wetland habitats separated by agricultural and urban areas (see Fig. 1). The conservation management of the HHL NIA aims to deliver the stated "more, bigger, better, and joined" ecological network within the landscape of the Humberhead wetlands, and these wetland habitats have been the focus of habitat creation and restoration work (wet grassland, reedbed, marsh, and wet woodland). To this end, in the first phase of management (2012–2015) 1190 ha (2.4% of the total area of the HHL NIA) of natural habitat was created, restored or extended (HLP 2015). The management of the HHL NIA has been a success in terms of increasing the extent and quality of target landcover categories represented across the landscape. In purely structural terms it appears that habitat is better connected, as the average distance between fragments of target land cover classes is lower than pre-management distances (Cruz et al. 2015). Here, we explore the functional connectivity enhancement that has resulted from the increase in habitat area, taking into account ecological processes.

Model species

Six species were chosen as appropriate indicators sensitive to connectivity enhancement in the HHL NIA: the azure damselfly (*Coenagrion puella*), common darter dragonfly (*Sympetrum striolatum*), water vole (*Arvicola amphibius*), grass snake (*Natrix natrix*), willow tit (*Poecile montanus*), and reed bunting (*Emberiza schoeniclus*). These species represented a range of different dispersal modes (insect and bird flight, plus mammal and reptile terrestrial movement), evolutionary histories (two invertebrates, two birds, one mammal and one reptile), habitat requirements (requiring a combination of aquatic, riparian and arboreal habitats, but all requiring water) and life-histories (short-lived invertebrates that live the majority of their lives in the water, vertebrates which reproduce annually and have overlapping generations). These species and their key traits are summarised in Table 1. A summary of the following hierarchical model structure can be found in Fig. S1.
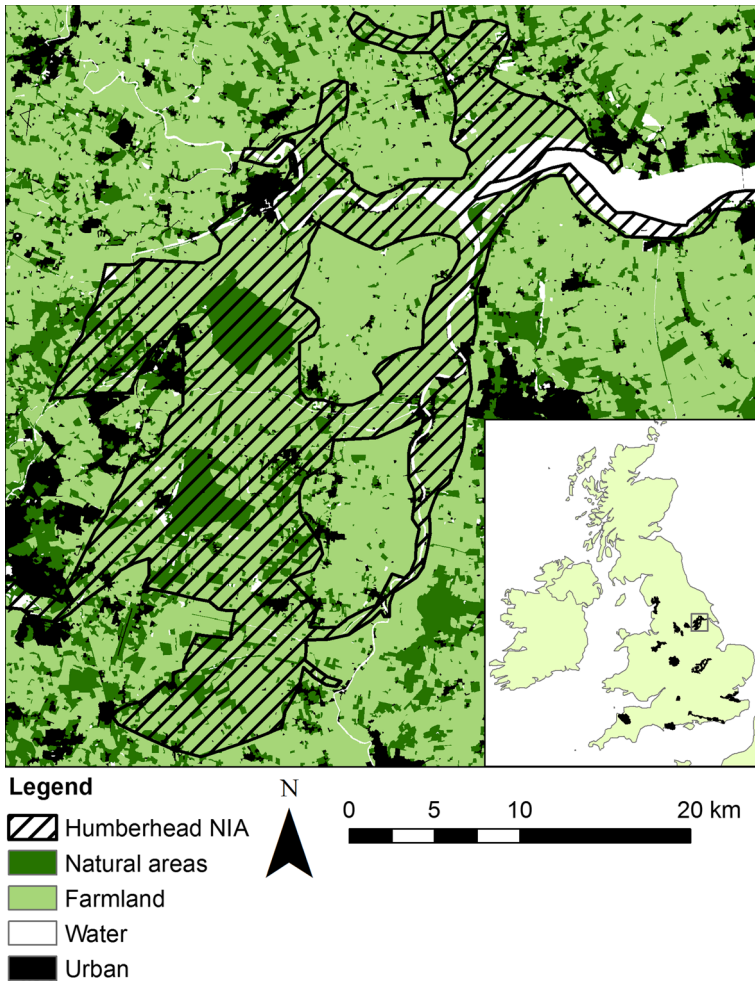
Fig. 1 Map of the Humberhead Levels Nature Improvement Area (NIA) in relation to natural habitat features (woodland, grassland, bog) and nearby urban areas. Map data are from Land Cover Map 2015 (Rowland et al. 2017) and NIA boundaries from Natural England (Natural England 2017). Inset map shows the context of the 11 NIAs in England and the location of the study site (rectangle)

Model 1: habitat suitability model

We used MaxEnt to produce habitat suitability surfaces for the focal species based on observations from biological records (Phillips et al. 2006). The minimum rectangular area that contained the full extent of the HHL NIA (45.9×43.8 km, 2010 km^2) was used as the focal area for all models. Species data from the ecological records in the Humberhead wetlands held by various parties (British Dragonfly Society, Doncaster Local Records Centre, North East Yorkshire Ecological Records Centre, National Biodiversity Network and British Trust for Ornithology) were used as model input. Merging of data from different sources was necessary as sample sizes received from each source individually were low,

Table 1 Indicator species considered and their relevant traits

Common name	Scientific name	Dispersal range	Habitat requirements	Inter-generation time	Fecundity
Reed bunting	*Emberiza schoeniclus*	0.95 km (SD 13.1 km) (Paradis et al. 1998)	Reed bed, wet grassland (Besnard et al. 2015), rank vegetation and open water (Brickle and Peach 2004)	1 year (Musilová et al. 2011)	Up to 5 (usually 2) clutches of 2–6 (usually 5) eggs (Pasinelli et al. 2008)
Willow tit	*Poecile montanus*	1.6 km (Orell et al. 1999)	Standing deadwood and shrub layer in wet woodland (Lewis et al. 2007)	1 year (Hogstad 2014)	1 clutch (7) of mean 6 eggs (Vatka et al. 2011)
Grass snake	*Natrix natrix*	17.3 ha ± 7.7 (males) 24.9 ha ± 18.2 (females) (adult range size) (Madsen 1984)	Ditches, nesting and hibernation sites (Löwenborg et al. 2012; Reading and Jofre 2009)	4 years (Madsen 1987)	1 clutch of 5–20 eggs (Madsen 1987)
Water vole	*Arvicola amphibius*	2.10 km (Sutherland et al. 2014)	Reed bed and Grazing marsh (MacPherson and Bright 2011)	1 year (Sutherland et al. 2012; Telfer et al. 2003)	3.41 of 6.1 young (Telfer et al. 2003)
Common darter dragonfly	*Sympetrum striolatum*	1.2 km (for *S. sanguineum*) (Conrad et al. 1999)	Warm standing water (Koch 2015a)	1 year (Koch 2015a)	Mean lifetime egg production 1041 (Koch 2015b)
Azure damselfly	*Coenagrion puella*	169 ± 22 m (Conrad et al. 2002)	High quality ponds and connecting habitat (Raebel et al. 2012)	1 year (Lowe et al. 2009)	3.85 (SD 2.89) clutches of 250 (± 150) eggs (Banks and Thompson 1985)

Fig. 2 Modifications to habitat quality for indicator species brought about by conservation management. ▶
The black line marks the HHL NIA boundary

with high spatial bias. As no duplicate records were found in these different databases, they
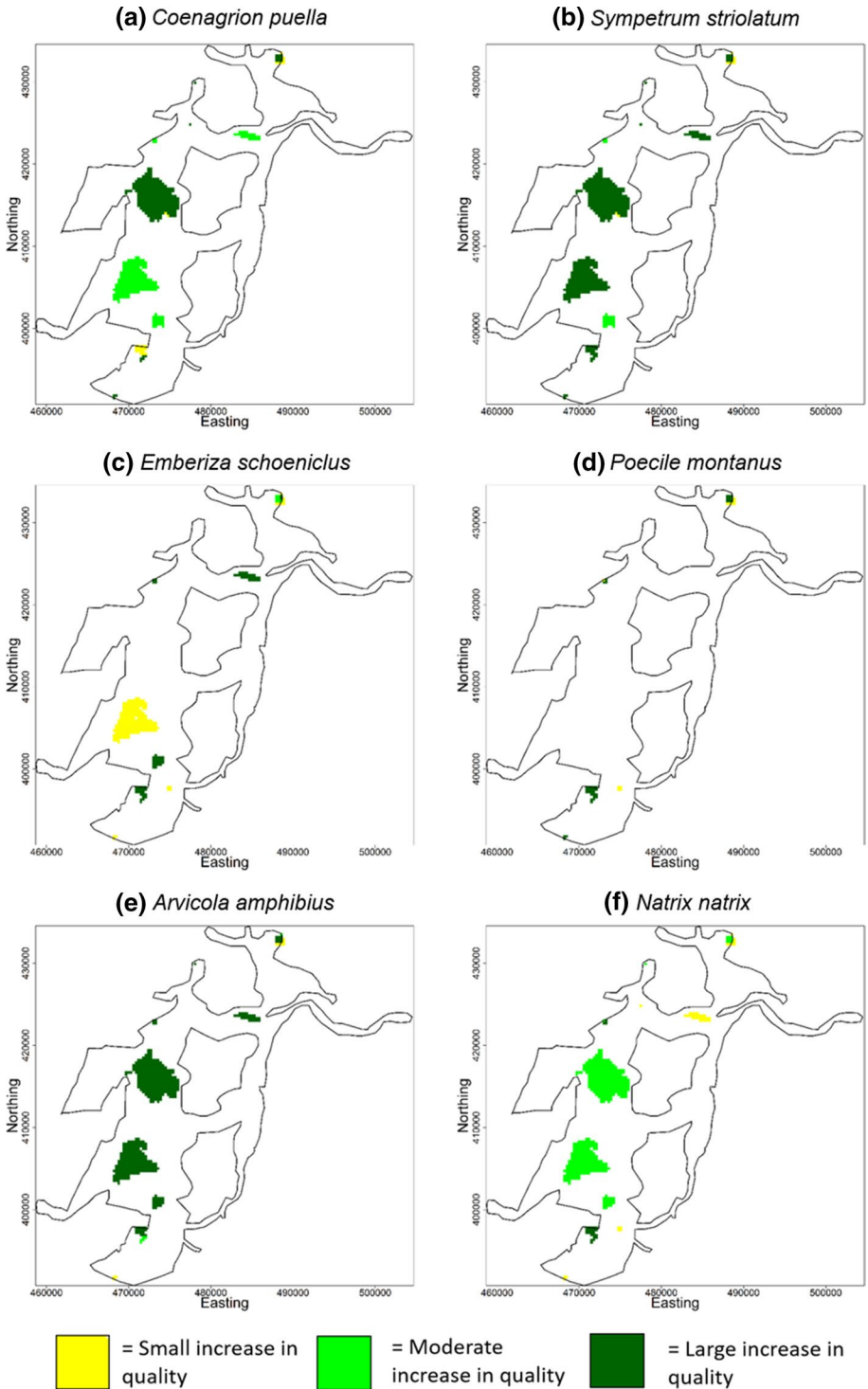were considered to be independent.

Species records were restricted temporally (2001–2016), spatially (to the extent of the
study area) and by resolution (≤ 100 m precision) using functions from the R package ras-
ter (Hijmans 2016; R Core Team 2016). Although landscape restoration work began in
2012 limiting records to pre-2012 resulted in too few records to produce good models.
As such we do not consider that baseline models represent "pre-management" conditions,
but rather represent conditions without considering management actions. Uneven sampling
effort can bias MaxEnt predictions, giving higher suitability scores to more intensively sur-
veyed sites (Hijmans 2012). Species presence datasets were spatially thinned to reduce the
effects of any sampling bias using the package SpThin (Aiello-Lammens et al. 2015) to
filter the data by imposing a minimum nearest neighbour distance of 300 m (odonates and
water voles, less mobile species) or 900 m (grass snake and birds, more mobile species).
Following this thinning the number of records used for each indicator species were: *Coena-
grion puella*: n = 83; *Sympetrum striolatum*: n = 139; *Emberiza schoeniclus*: n = 52; *Peocile
montanus*: n = 18; *Arvicola amphibius*: n = 149; *Natrix natrix*: n = 25.

Twenty-five environment layers, rasterised to a 300 m cell size, were used as the land-
scape inputs for habitat suitability models using MaxEnt v3.3.3 k (Dudik et al. 2004). The
layers represented land cover, elevation, bioclimatic variables (from WorldClim, Hijmans
et al. 2005) and density of linear features: roads, railways, rivers and agricultural ditches
(see Online Resource, Appendix A and Figure S2). Parameterisation of MaxEnt models
followed the procedure of Mazor et al. (2016) for settings see Online Appendix B.

In order to represent the local-scale changes to the HHL NIA landscape, spatially
explicit management data were retrieved from the Biodiversity Actions Recording Service
(BARS). This dataset represents the landscape modifications during phase 1 of the HHL
NIA management program (2011–2015). Each management action was ranked in terms
of the local effect on habitat quality for each species individually. Actions were ranked
from zero (no effect) to three (large increase in quality) based on the expert opinion of
four conservation practitioners involved in designing and delivering the interventions. The
resulting habitat modifications for each species are shown in Fig. 2. Ranked data for habitat
improvement were converted to a 0–0.3 scale to match the MaxEnt scale. The manage-
ment-modified habitat suitability maps were generated by summing the MaxEnt outputs
and management modification rasters (maximum suitability limited to 1).

Model 2: individual-based models

In order to identify the functional responses of our indicator species to the habitat struc-
ture provided by MaxEnt models we used spatially explicit individual-based models. These
models simulate the actions of every individual within a metapopulation with their behav-
iour determined jointly by life-history parameters and conditions determined by a set of
spatial inputs (van der Vaart et al. 2016). The habitat suitability maps generated by Max-
Ent were the basis of the spatial inputs used for three key components of individual-based
models constructed in RangeShifter v1.0.5 (Bocedi et al. 2014a): a habitat quality map that
used the MaxEnt output rescaled to a 0–100 scale with cell values representing the percent-
age of maximum carrying capacity that the cell can support; a patch layer defined such that

(a) *Coenagrion puella*

(b) *Sympetrum striolatum*

(c) *Emberiza schoeniclus*

(d) *Poecile montanus*

(e) *Arvicola amphibius*

(f) *Natrix natrix*

= Small increase in quality

= Moderate increase in quality

= Large increase in quality

cells with a habitat suitability < 0.5 became inter-habitat matrix and those with a suitability ≥ 0.5 habitat (Liu et al. 2005); and a cost surface, with cell values representing the difficulty a dispersing animal has moving through the cell, was created based on a reciprocal transformation of habitat suitability (after adding 0.1 to limit maximum resistance to 10) resulting in a scale of matrix hostility of 2–10 (all habitat had a resistance of 1).

Demographic and behavioural parameters were drawn from a literature search. A table of parameter values used in RangeShifter models is given in Online Appendix D. Transfer between habitat patches was modelled using the Stochastic Movement Simulator (Palmer et al. 2011), embedded in RangeShifter (Aben et al. 2016). The dispersal parameters generated realistic dispersal kernel patterns at the population scale, while allowing stochastic, cost-directed movement decisions at the individual level (see Online Appendix C for details).

Initialisation and evaluation

Baseline models were initialised with all patches occupied at carrying capacity. Fifty replicates of each model were run. After a 99 year burn-in, values for the 100th simulation year taken across the 50 replicates were used as final output (means for population size, population density, dispersal distances and number of dispersers while occupancy was taken as the proportion of replicates in which a habitat patch had a non-zero population). Management models, those using the management-modified MaxEnt outputs, were initialised to reflect the population structure in baseline outputs. Only habitat patches with occupancy rates of ≥ 0.5 in baseline outputs were seeded and starting density within patches was set so that the management population at initialisation matched baseline output populations. In order to establish stable population dynamics (i.e. when population size and occupancy rates are reasonably stable) a 19 year burn-in was required. Final output was taken for the 20th simulation year, by which time stable population structure was established for all species, as for the baseline models for the 100th year. Due to the uncertain effect of the burn-in time, outputs can only be considered broadly applicable to conditions in the HHL NIA 5–20 years following management actions. In order to assess the effect of innaccuracy defining demographic input parameter values, sensitivity analyses were conducted for both baseline and management models (Online Resource, Appendix H). T-tests were used to identify significant differences ($p < 0.05$) between baseline and management models in landscape-summarised outputs: landscape transfer (the total number of individuals moving from one habitat patch and settling in another), mean distance moved by dispersing individuals and total population size in the final simulation year. Spatially-explicit changes in landscape connectivity were evaluated visually through the examination of network plots (Fig. 7, Online Resource, Appendix G).

Field surveys

In order to validate model outputs, field surveys were undertaken in 2017. Transect surveys for *Arvicola amphibius* were designed to cover 20 of the 300 × 300 m cells used in the models, using a stratified-random sampling method (Southwood and Henderson 2000) to ensure that the range of habitat suitability predictions made by the baseline MaxEnt models was represented (five survey cells per quartile of habitat suitability scale). Based on Ordinance Survey maps and satellite images, transects were drawn in each of the survey cells to cover all potential vole habitat. Surveys focused on searching for field signs to

identify presence/absence within survey cells, as per standard water vole monitoring methods (MacPherson and Bright 2011). Logistic regressions were calculated in R using the drc package (Ritz et al. 2015) to compare presences detected in the survey cells with model predictions of habitat suitability (0–1 habitat score output by MaxEnt), occupancy (proportion of model replicates in which the habitat patch has a population ≥ 1), and population density (mean number of individuals per cell in a habitat patch across all model replicates) in the survey cells.

Results

MaxEnt outputs

The test AUC and standard deviations output by MaxEnt were: *Coenagrion puella* AUC $= 0.737 \pm 0.045$ (SD), *Sympetrum striolatum* 0.796 ± 0.041, *Emberiza schoeniclus* 0.657 ± 0.059, *Peocile montanus* 0.671 ± 0.073, *Arvicola amphibius* 0.807 ± 0.033, *Natrix natrix* 0.826 ± 0.112. Figure 3 shows example outputs for *Arvicola amphibius*, the raw MaxEnt output, the management modified output and the RangeShifter spatial inputs based on these layers. Figures for other species are provided in Online Resources (Figs. S5–10). Table 2 shows the impacts of NIA management on the available habitat for each study species (defining habitat as areas of > 0.5 habitat suitability in models).

Individual-based model outputs

The pattern of connectivity predicted across the landscape for each indicator species is shown in Fig. 4 for baseline models and Fig. 5 for management models. The connections between habitat patches represent a prediction of functional connectivity (the successful exchange of individuals between habitat patches). *Coenagrion puella*, *Emberiza schoeniclus*, *Peocile montanus* and *Arvicola amphibius* (Fig. 4b–e) display a series of functionally isolated clusters, whereas *Sympetrum striolatum* and *Natrix natrix* are strongly connected across their predicted range. However, significant bottlenecks are predicted in the *Sympetrum striolatum* network and *Natrix natrix* is restricted to a corner of the landscape (Fig. 4a, f).

Evaluating management impacts

Landscape-summarised outputs are shown in Fig. 6. The models predict a significant increase in the landscape transfer of individuals for all modelled species except *Coenagrion puella* and *Peocile montanus*. The same pattern can be seen in overall population size, except here *Coenagrion puella* also shows a significant increase. Mean dispersal distance also shows a significant increase in management models for all species except *Peocile montanus*.

Figure 7 shows the changes in patch connections due to management interventions. A number of inter-patch connections are expected to be enhanced or created (as shown in green) by management efforts (with the exception of *Peocile montanus*). However, the pattern of connections across the landscape is not greatly different to that of baseline models (Fig. 4). Rather than new connections being created in management models, the main
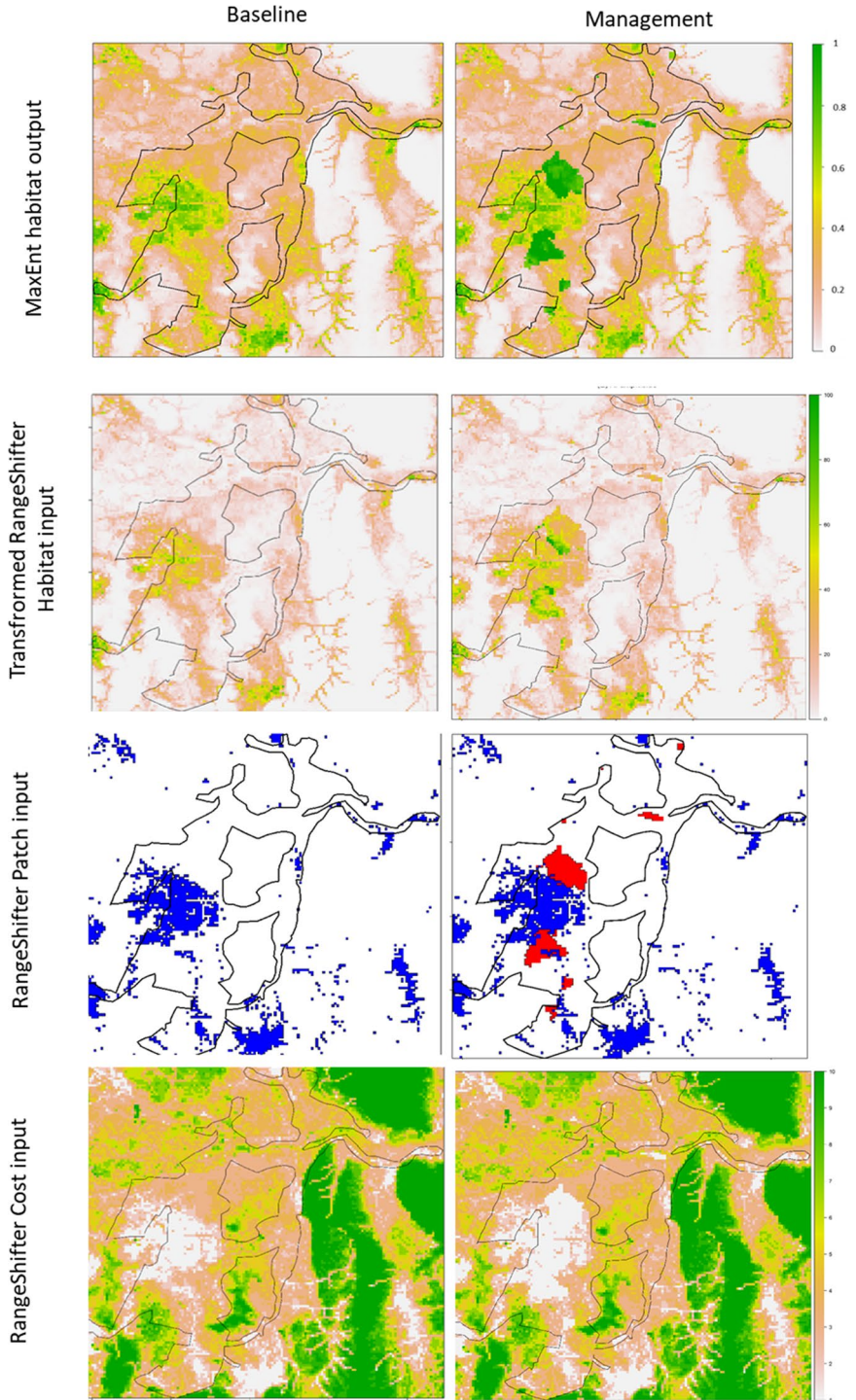
Fig. 3 MaxEnt outputs and RangeShifter spatial inputs for *Arvicola amphibius*. For the patch inputs, blue indicates habitat present in the baseline models and red extensions/new habitat patches created through management

Table 2 Management area and the effects on habitat area

Species	Area of management impact/ha	Baseline habitat area/ha	Management habitat area/ha	New habitat created/ha
Coenagrion puella	15,290	13,100	16,010	2910 (+22%)
Sympetrum striolatum	15,290	10,990	13,220	2232 (+20%)
Emberiza schoeniclus	2020	13,180	13,710	531 (+4.0%)
Poecile montanus	250	11,910	12,200	297 (+2.5%)
Arvicola amphibius	14,980	15,810	19,290	3474 (+22%)
Natrix natrix	13,580	6020	6800	783 (+13%)

benefits predicted are the buffering and enhancement of existing functional connections across the landscape.

Field surveys

Eighteen sites were surveyed for *Arvicola amphibius* between 20th April and 6th July 2017, with two of the planned sites not accessible due to poor weather. Presence and absence results are compared with patch-based population predictions from models (for full outputs see Online Appendix G) in Fig. 8. Logistic regressions indicate baseline population density was the best predictor of species presence in field surveys. Presence was also predicted better by the outputs of models such as occupancy and population density than by habitat suitability alone (Table 2, Fig. 8).

Discussion

This study (and the related work by Cruz et al. 2015) represents the first quantitative evaluation of practical interventions stemming from recommendations put forward in the Lawton Review of landscape management (Lawton 2010). The specific aim was to evaluate the landscape management of the HHL NIA with regard to increasing ecological connectivity. This evaluation was conducted through ecologically representative hybrid models for six indicator species in the HHL NIA. These models combined species-specific habitat suitability models with spatially-explicit, individual-based dispersal and population models.

The stated aims of the HHLs management plan, based on Lawton (2010), are to create a bigger, better and more connected ecological network (HLP 2015). The models suggest that these targets have been met to some degree, as management has increased the area of habitat for five modelled species (although not for *Peocile montanus*) (see Fig. 6, Table 3). Population growth and increased landscape transfer are predicted at the landscape scale as a result of this. However, the lack of impact for a key management target species (*Peocile montanus*), likely due to a limited area of habitat enhancement for this species (see Fig. 7), suggests that the NIA management may not have targeted this nationally declining habitat specialist adequately (Lewis et al. 2007).

Despite being driven by the best readily available data, the relevance of these model outputs depend upon the accuracy of these data and the relevance of several assumptions made during the modelling process (MacPherson and Gras 2016). As such, independent empirical data was sought to validate model predictions via field surveying of
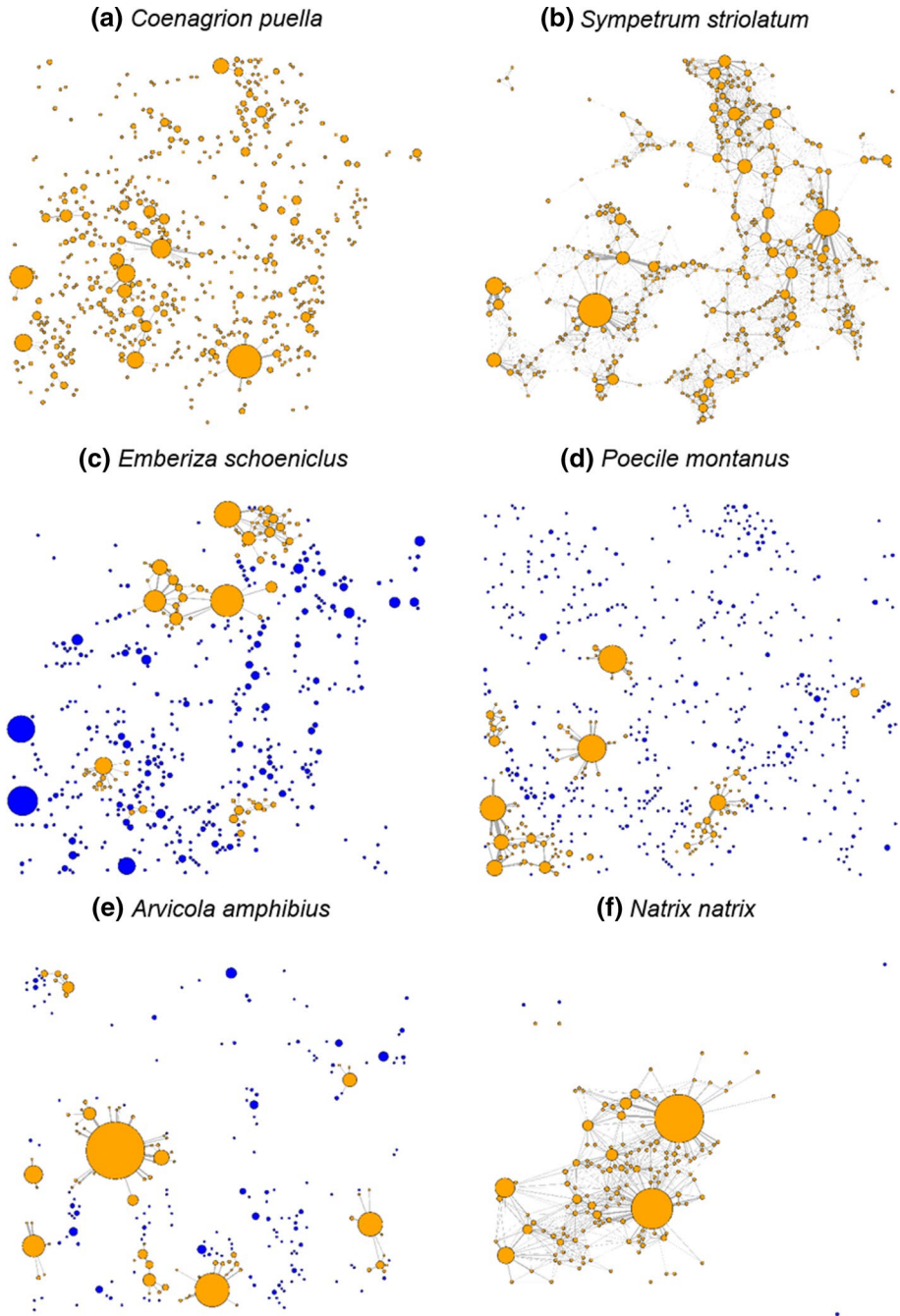
Fig. 4 Connectivity output from baseline models. Circles represent habit patches and lines represent the number of animals exchanged between habitat patches per year. Circle size indicates patch area and line width the number of animals exchanged. Colour represents occupancy (blue for occupancy < 0.5 and orange for occupancy of > 0.5)
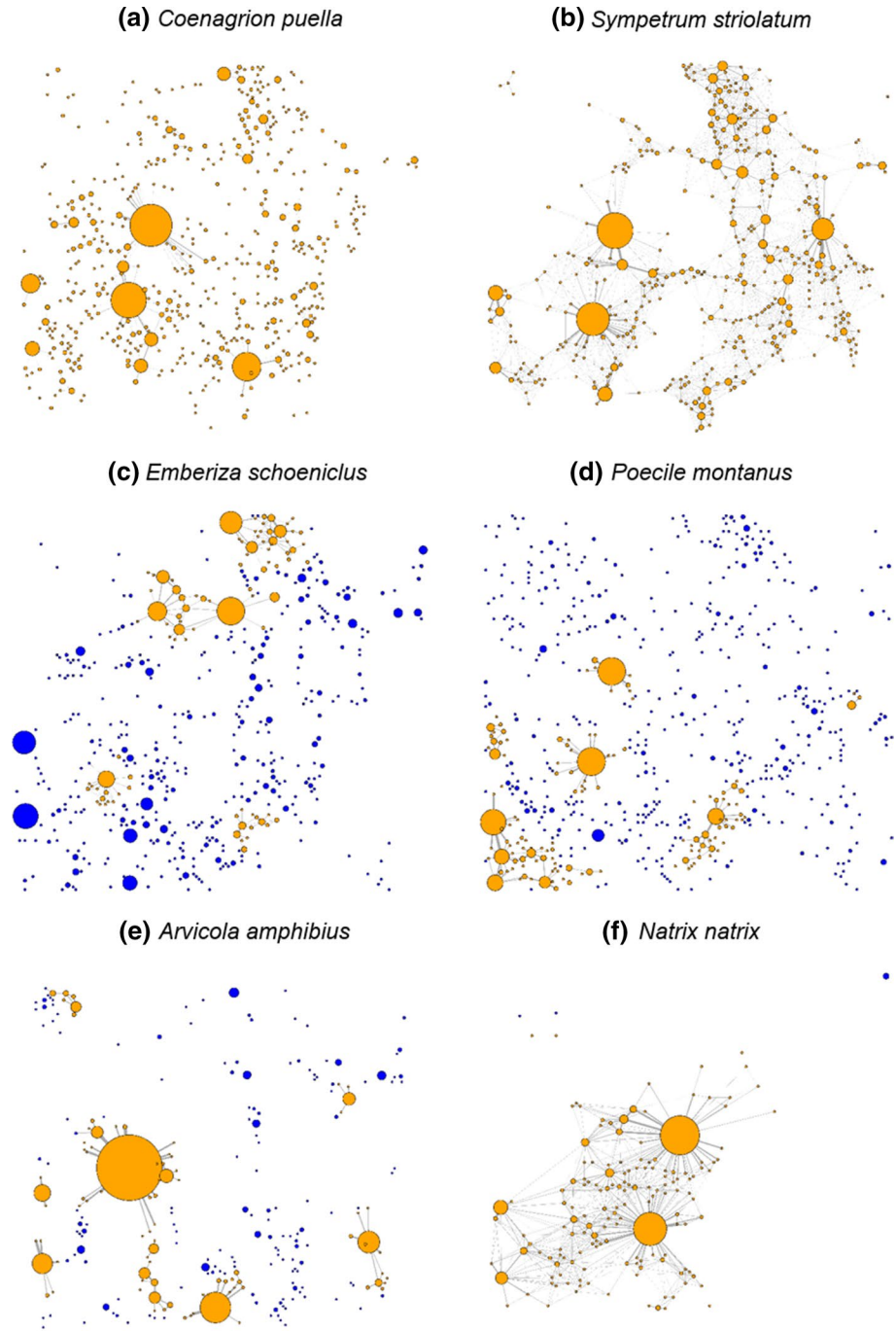
(a) *Coenagrion puella*　　　　　**(b)** *Sympetrum striolatum*

(c) *Emberiza schoeniclus*　　　　**(d)** *Poecile montanus*

(e) *Arvicola amphibius*　　　　　**(f)** *Natrix natrix*

Fig. 5 Connectivity output from management models. Circles represent habit patches and lines indicate the number of animals exchanged between habitat patches per year. Circle size represents patch area and line with the number of animals exchanged. Colour represents occupancy (blue for occupancy < 0.5 and orange for occupancy > 0.5)
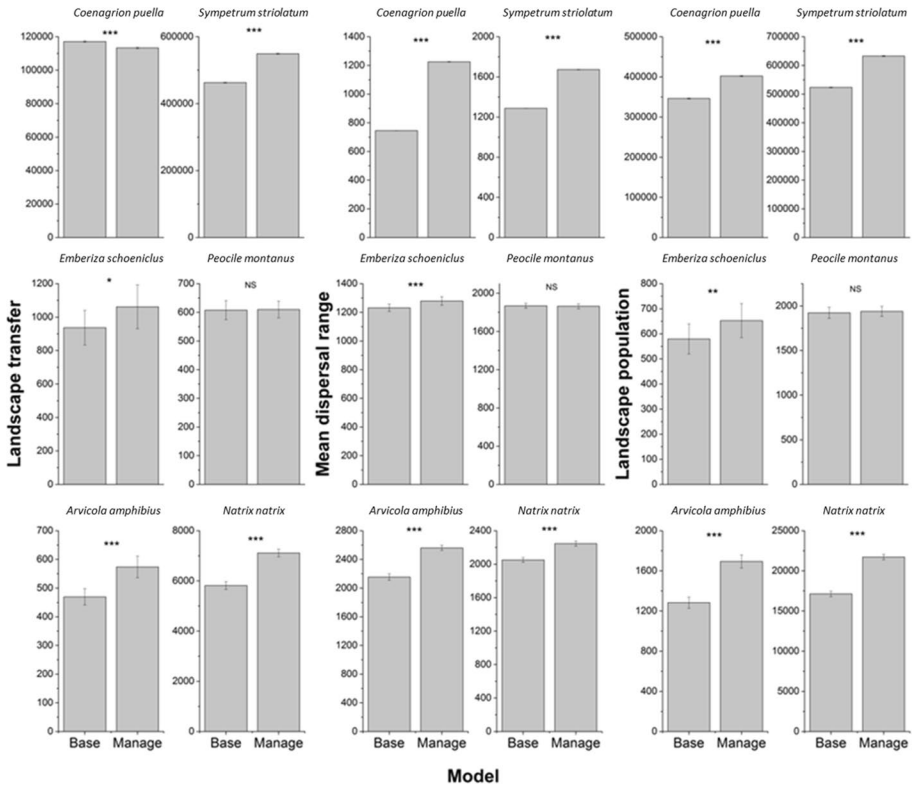
Fig. 6 Differences between baseline ("base") and post-management ("manage") models in landscape transfer, mean dispersal range, and landscape population. *NS* non-significant, *p < 0.05, **p < 0.01, ***p < 0.001. Error bars represent ± one standard deviation

the modelled landscape. While provisional in scope, the data collected lends tentative support to the accuracy of model predictions and thus the validity of model structure, if not the response to management modifications (though this is likely due to the limited time since management actions were completed). Repeating the surveys over multiple field seasons would have allowed a confident assessment of whether management changes are having an impact, but we did not have the time or funding for multi-year field surveys.

The simulated dynamics for *Arvicola amphibius* fit previous work by MacPherson and Bright (2011) modelling metapopulation structure in this species, in that a few large fragments of habitat are predicted to support metapopulation dynamics and maintain populations in smaller fragments. Genetic studies of vole metapopulations have found a high degree of genetic differentiation by distance between populations, supporting the model prediction that these large habitat fragments are functionally isolated from each other over large distances (Melis et al. 2013). These results provide vital information for supporting the conservation management of this species, which has undergone serious declines in the UK due to habitat loss and predation by invasive American mink, *Neovision vision* (Strachen 2004). As such, the creation and/or maintenance of large
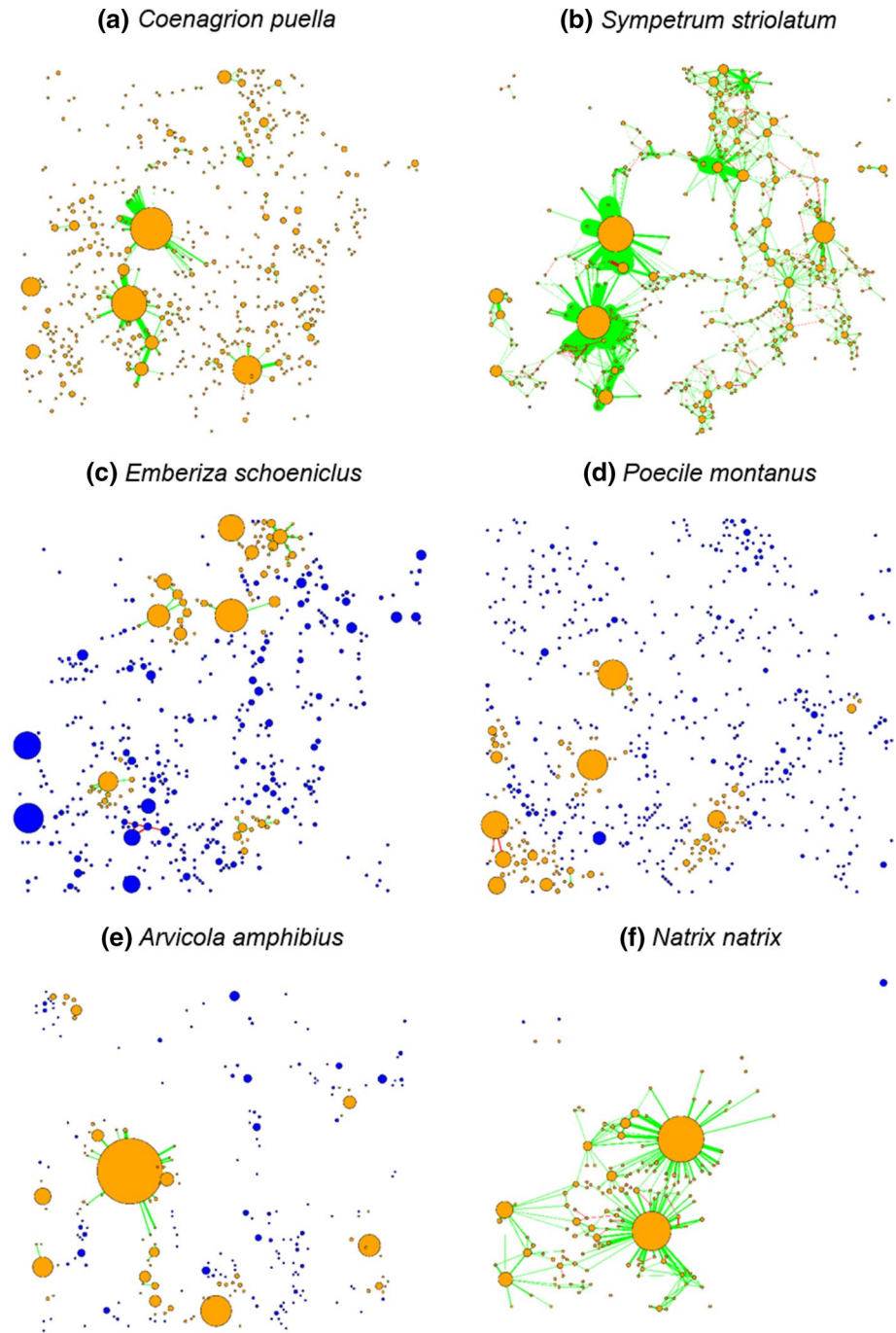
(a) *Coenagrion puella*

(b) *Sympetrum striolatum*

(c) *Emberiza schoeniclus*

(d) *Poecile montanus*

(e) *Arvicola amphibius*

(f) *Natrix natrix*

Fig. 7 Change in connectivity between baseline and management outputs. Circles represent habit patches and lines show change in individuals exchanged. Circle size indicates patch area and line width the difference in number of animals exchanged between baseline and management models. Blue nodes indicates occupancy < 0.5 and orange for occupancy > 0.5 in management models. Green lines indicate an increase in movement for management models and red a decrease
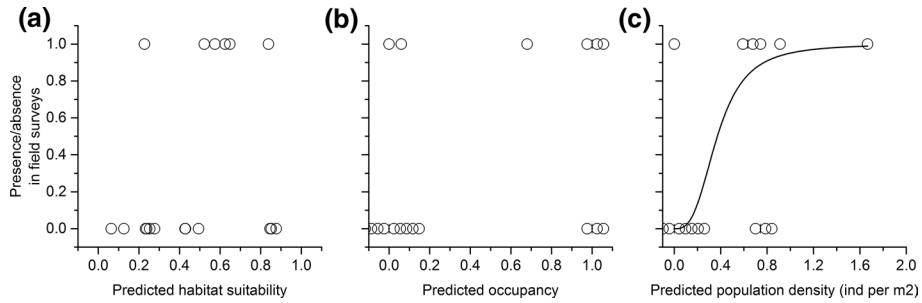
Fig. 8 Presence–absence results of field surveys for *Arvicola amphibius* against baseline model predictions. Overlapping points are separated along the x-axis for clarity. The model fit relates to the statistically significant model (see Table 3 for more details)

Table 3 *Arvicola amphibius* logistic regressions comparing baseline and management model ability to predict survey results

Treatment	Predictor	Estimate	SE	Z-value	p-value
Baseline	Habitat suitability	2.270	2.057	1.104	0.270
	Occupancy	1.792	1.093	1.639	0.101
	Population density	3.314	1.625	2.039	0.041*
Management	Habitat suitability	2.529	2.195	1.152	0.249
	Occupancy	1.792	1.093	1.639	0.101
	Population density	2.592	1.511	1.716	0.086

*Statistical significance at p = 0.05

fragments of reedbed and grazing marsh, and the promotion of connections between these fragments are of vital importance to this species.

One unexpected and potentially problematic result is the significant difference in mean dispersal range between baseline and management models, as dispersal ranges predicted in management models no longer fit empirical estimates as intended (see Online Appendix C). However, when landscape structure changes species traits will not change, but interaction with a novel landscape structure may create novel, emergent patterns, such as a change in the realised dispersal range of species. As the management landscapes do not represent typical fragmentation patterns as closely as baseline landscapes, it might be expected that "less typical" dispersal ranges are observed. Furthermore, empirical measurement of dispersal kernels is often confounded by logistics, particularly study area size (Hassall and Thompson 2012) making the quantification of long distance movements particularly difficult (Trakhtenbrot et al. 2005). Empirical studies have demonstrated that measured dispersal distances are to some degree determined by levels of habitat fragmentation (Mayer et al. 2009). As such we believe that dispersal kernels should not necessarily be conserved when landscape structure has changed, meaning that our simulations may still be realistic, although they should be treated with a note of caution.

Management implications

The evaluation of management actions is generally positive, indicating success in enhancing connectivity within submodules of the landscape habitat network. However, these benefits

have not extended to every indicator species considered, as the nationally declining *Peocile montanus* was not predicted to see similar benefits as other species. This appears to be a result of poor targeting of woodland habitat that, although relatively scarce across the HHL NIA (HLP 2015), is a key requirement for this species (Hogstad 2014). In addition, there are limitations to the benefits predicted for other indicator species considered, suggesting that the management actions have been poorly focused to reconnect functionally isolated elements of the habitat network for key species. This highlights the need to target management interventions more carefully in order to create dispersal corridors that reconnect functionally isolated elements of species' habitat networks, similar to recommendations made in other studies (Conlisk et al. 2014; Benz et al. 2016).

By simulating populations across the landscape we have gone further than most analyses of functional connectivity by considering the effects of population dynamics, meaning we were able to generate predictions of realised connectivity (Wiegand et al. 2004). The species-specific, bottom-up approach used offers biologically representative modelling based on explicit consideration of species attributes, from the first stages of model construction, informed by current ecological theory. Although the approaches used here provide a strong framework for estimating metapopulation and connectivity patterns in an ecologically meaningful manner, these models require further development and refinement. With more detailed ecological data more robust habitat models could be constructed (Guillera-Arroita et al. 2015) and density-dependent processes could be incorporated into individual-based models (Bocedi et al. 2014b).

The main limitation of connectivity management within the Humberhead Levels NIA appears to have been due to the practical necessity of most of the conservation effort occurring within existing natural or managed areas (Humberhead Levels Partnership 2015). Although working within existing natural areas reduces many costs and problems (e.g. land acquisition costs, access costs and increased investment needed to restore truly degraded areas), here we see the limitations of this. As the landscape modifications within the Humberhead Levels have largely enhanced existing habitat, rather than created new habitat patches (Fig. 2, Online Appendix F Fig. S9), meaning that no major restructuring, such as the creation of migration corridors etc., has occurred. To create these enhanced connections it may be necessary to work outside of existing wild networks and invest resources in rewilding degraded areas and/or focus on the removal of dispersal barriers in the landscape (Ziółkowska et al. 2016). However, such actions are not trivial and should be carefully planned. We suggest that the kinds of models used here may be equally useful alongside systematic conservation planning approaches that incorporate costs and benefits to generate hypothetical protected area networks. Subsequent analysis for connectivity as presented in this study could facilitate an iterative process of reserve design that could be used to optimise connectivity in a cost effective and ecologically effective manner before resources are invested on the ground (Allen et al. 2016). While a limitation of the approach is the paucity of species-specific data, we feel that the application of a keystone or indicator species approach such as that presented here would go some way towards producing meaningful, functional connectivity evaluations that are representative across many taxa.

Conclusion

In order to assess the landscape scale impacts of management in the HHL NIA, a model framework has been developed with a novel combination of features, namely (i) use of a recently developed individual based metapopulation modelling platform, RangeShifter; (ii) multiple focal species and large spatial extent of the study for an individual based model; (iii) dispersal parameterisation using the Stochastic Movement Simulator; and (iv) application of a hybrid model framework to assess connectivity without a climate change or range shift aspect. By considering species-specific biology from the first stages and simulating ecological processes in a bottom-up manner, simulation models were created that can replicate natural patterns. These models produced detailed predictions of structure and connectivity for each indicator species considered, which have allowed evaluation of management efforts in the landscape. These predictions, and the methods developed to produce them, should be valuable in informing the future management of the HHL NIA. Through further development and elaboration these methods can be usefully applied to both evaluating and planning landscape-scale conservation for connectivity enhancement, among other potential objectives.

Author contributions CH conceived the idea for the study. CH and JH-A designed methodology. JH-A ran the models, collected the field data, and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

References

Aben J, Bocedi G, Palmer SC et al (2016) The importance of realistic dispersal models in conservation planning: application of a novel modelling platform to evaluate management scenarios in an Afrotropical biodiversity hotspot. J Appl Ecol 53:1055–1065. https://doi.org/10.1111/1365-2664.12643

Aiello-Lammens ME, Boria RA, Radosavljevic A et al (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545. https://doi.org/10.1111/ecog.01132

Allen CH, Parrott L, Kyle C (2016) An individual-based modelling approach to estimate landscape connectivity for bighorn sheep (Ovis canadensis). PeerJ 4:e2001. https://doi.org/10.7717/peerj.2001

Banks MJ, Thompson DJ (1985) Emergence, longevity and breeding area fidelity in *Coenagrion puella* (L.) (Zygoptera: coenagrionidae). Odonatologica 14:279–286

Benz RA, Boyce MS, Thurfjell H et al (2016) Dispersal ecology informs design of large-scale wildlife corridors. PLoS ONE 11:e0162989. https://doi.org/10.1371/journal.pone.0162989

Besnard AG, Davranche A, Maugenest S et al (2015) Vegetation maps based on remote sensing are informative predictors of habitat selection of grassland birds across a wetness gradient. Ecol Indic 58:47–54. https://doi.org/10.1016/j.ecolind.2015.05.033

Bocedi G, Palmer SCF, Peer G et al (2014a) RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. Methods Ecol Evol 5:388–396. https://doi.org/10.1111/2041-210x.12162

Bocedi G, Zurell D, Reineking B, Travis JMJ (2014b) Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. Ecography 37:1240–1253. https://doi.org/10.1111/ecog.01041

Brickle NW, Peach WJ (2004) The breeding ecology of Reed Buntings Emberiza schoeniclus in farmland and wetland habitats in lowland England. Ibis 146:69–77

Carvajal-Quintero JD, Januchowski-Hartley SR, Maldonado-Ocampo JA et al (2017) Damming fragments species' ranges and heightens extinction risk. Conserv Lett 10:708–716. https://doi.org/10.1111/conl.12336

Chaput-Bardy A, Lemaire C, Picard D, Secondi J (2008) In-stream and overland dispersal across a river network influences gene flow in a freshwater insect, *Calopteryx splendens*. Mol Ecol 17:3496–3505. https://doi.org/10.1111/j.1365-294X.2008.03856.x

Conlisk E, Motheral S, Chung R et al (2014) Using spatially-explicit population models to evaluate habitat restoration plans for the San Diego cactus wren (*Campylorhynchus brunneicapillus sandiegensis*). Biol Conserv 175:42–51. https://doi.org/10.1016/j.biocon.2014.04.010

Conrad KF, Wilson KH, Harvey IF et al (1999) Dispersal charicteristics of seven odonate species in an agricultural landscape. Ecography 22:524–531

Conrad KF, Wilson KH, Whitfield K et al (2002) Charicteristics of dispersing *Ischnura elegans* and *Coenagrion puella* (Odonata): age, sex, size, morph and ectopatisitism. Ecography 25:439–445

Crawford JA, Semlitsch RD (2007) Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. Conserv Biol 21:152–158. https://doi.org/10.1111/j.1523-1739.2006.00556.x

Cruz J, McClean C, White P (2015) Development of connectivity indicators to evaluate the landscape-scale impact of the Humberhead Levels Nature Improvement Area. University of York. Unpublished thesis

Dudik M, Phillips SJ, Schapire RE (2004) Performance guarantees for regularized maximum entropy density estimation. In: ShaweTaylor J, Singer Y (eds) Learning Theory, Proceedings. Springer, Berlin, pp 472–486

England N (2017) Nature improvement areas. http://naturalengland-defra.opendata.arcgis.com/datasets/nature-improvement-areas-england

Eros T, Olden JD, Schick RS et al (2012) Characterizing connectivity relationships in freshwaters using patch-based graphs. Landsc Ecol 27:303–317. https://doi.org/10.1007/s10980-011-9659-2

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J et al (2015) Is my species distribution model fit for purpose? Matching data and models to applications. Glob Ecol Biogeogr 24:276–292. https://doi.org/10.1111/geb.12268

Hassall C, Thompson DJ (2012) Study design and mark-recapture estimates of dispersal: a case study with the endangered damselfly *Coenagrion mercuriale*. J Insect Conserv 16:111–120. https://doi.org/10.1007/s10841-011-9399-2

Heino J, Melo AS, Siqueira T et al (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshw Biol 60:845–869. https://doi.org/10.1111/fwb.12533

Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93:679–688

Hijmans RJ (2016) raster: geographic data analysis and modeling. R package version 2.5-8

Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. https://doi.org/10.1002/joc.1276

Hodgson JA, Thomas CD, Cinderby S et al (2011) Habitat re-creation strategies for promoting adaptation of species to climate change. Conserv Lett 4:289–297. https://doi.org/10.1111/j.1755-263X.2011.00177.x

Hogstad O (2014) Ecology and behaviour of winter floaters in a sunalpine population of willow tits, Poecile montanus. Ornis Fenn 91:29–38

Humberhead Levels Partnership (2015) Humberhead levels nature improvement area Phase 1 report

Koch K (2015a) Lifetime egg production of captive libellulids (Odonata). Int J Odonatol 18:193–204. https://doi.org/10.1080/13887890.2015.1043656

Koch K (2015b) Influence of temperature and photoperiod on embryonic development in the dragonfly *Sympetrum striolatum* (Odonata: Libellulidae). Physiol Entomol 40:90–101. https://doi.org/10.1111/phen.12091

Lawson DM, Regan HM, Zedler PH, Franklin J (2010) Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. Glob Chang Biol. https://doi.org/10.1111/j.1365-2486.2009.02143.x

Lawton J (2010) Making space for nature: a review of england's wildlife sites and ecological network. Department for Food, Agriculture and Rural Affairs, London

Lewis AJG, Amar A, Cordi-Peic D, Thewlis RM (2007) Factors influencing willow tit Poecile montanus site occupancy: a comparison of abandoned and occupied woods. Ibis 149:205–213

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurance in the prediction of species distributions. Ecography 28:385–393

Lowe CD, Harvey IF, Watts PC, Thompson DJ (2009) Reproductive timing and petterns of development for the damselfly *Coenagrion puella* in the field. Ecology 90:2202–2212

Löwenborg K, Kärvemo S, Tiwe A, Hagman M (2012) Agricultural by-products provide critical habitat components for cold-climate populations of an oviparous snake (*Natrix natrix*). Biodivers Conserv 21:2477–2488. https://doi.org/10.1007/s10531-012-0308-0

Luque S, Saura S, Fortin M-J (2012) Landscape connectivity analysis for conservation: Insights from combining new methods with ecological and genetic data. Landsc Ecol 27:153–157. https://doi.org/10.1007/s10980-011-9700-5

MacPherson JL, Bright PW (2011) Metapopulation dynamics and a landscape approach to conservation of lowland water voles (*Arvicola amphibius*). Landsc Ecol 26:1395–1404. https://doi.org/10.1007/s10980-011-9669-0

MacPherson B, Gras R (2016) Individual-based ecological models: adjunctive tools or experimental systems? Ecol Modell 323:106–114. https://doi.org/10.1016/j.ecolmodel.2015.12.013

Madsen T (1984) Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweeden. Copeia 1984:707–713

Madsen T (1987) Cost of reproduction and female life-history tactics in a population of grass snakes, *Natrix natrix*, in southern Sweeden. Oikos 49:129–132

Mayer C, Schiegg K, Pasinelli G (2009) Patchy population structure in a short-distance migrant: evidence from genetic and demographic data. Mol Ecol 18:2353–2364. https://doi.org/10.1111/j.1365-294X.2009.04200.x

Mazor T, Beger M, McGowan J et al (2016) The value of migration information for conservation prioritization of sea turtles in the Mediterranean. Glob Ecol Biogeogr 25:540–552. https://doi.org/10.1111/geb.12434

Melis C, Borg ÅA, Jensen H et al (2013) Genetic variability and structure of the water vole *Arvicola amphibius* across four metapopulations in northern Norway. Ecol Evol 3:770–778. https://doi.org/10.1002/ece3.499

Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography (Cop) 36:1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Musilová Z, Musil P, Fuchs R, Poláková S (2011) Territory settlement and site fidelity in reed buntings *Emberiza schoeniclus*. Bird Study 58:68–77. https://doi.org/10.1080/00063657.2010.524915

Orell M, Lahti K, Koivula K et al (1999) Immigration and gene flow in a northern willow tit (*Parus montanus*) population. J Evol Biol 12:283–295

Palmer SCF, Coulon A, Travis JMJ (2011) Introducing a "stochastic movement simulator" for estimating habitat connectivity. Methods Ecol Evol 2:258–268. https://doi.org/10.1111/j.2041-210X.2010.00073.x

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. J Anim Ecol 67:518–536

Parrott L (2011) Hybrid modelling of complex ecological systems for decision support: Recent successes and future perspectives. Ecol Inform 6:44–49. https://doi.org/10.1016/j.ecoinf.2010.07.001

Pasinelli G, Mayer C, Gouskov A, Schiegg K (2008) Small and large wetland fragments are equally suited breeding sites for a ground-nesting passerine. Oecologia 156:703–714. https://doi.org/10.1007/s00442-008-1013-2)

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 190:231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

R Core Team (2016) R: a language and environment for statistical computing

Raebel EM, Merckx T, Feber RE et al (2012) Identifying high-quality pond habitats for Odonata in lowland England: implications for agri-environment schemes. Insect Conserv Divers 5:422–432. https://doi.org/10.1111/j.1752-4598.2011.00178.x

Reading CJ, Jofre GM (2009) Habitat selection and range size of grass snakes *Natrix natrix* in an agricultural landscape in southern England. Amphibia-Reptilia 30:379–388

Ritz C, Baty F, Streibig JC, Gerhard D (2015) Dose-response analysis using R. PLoS ONE 10:1–13. https://doi.org/10.1371/journal.pone.0146021

Rowland CS, Morton RD, Carrasco L, McShane G, O'Neil AW, Wood CM (2017) Land cover map 2015 (25m raster, GB). NERC Environmental Information Data Centre. https://doi.org/10.5285/bb15e 200-9349-403c-bda9-b430093807c7, https://catalogue.ceh.ac.uk/documents/bb15e200-9349-403c-bda9-b430093807c7

Simpkins CE, Dennis TE, Etherington TR, Perry GLW (2018) Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach. Ecol Modell 367:13–23. https://doi.org/10.1016/j.ecolmodel.2017.11.001

Southwood R, Henderson PA (2000) Ecological methods. Blackwell Publishing Ltd, Hoboken

Strachen R (2004) Conserving water voles: Britain's fastest declining mammal. Water Environ J 18:1–4

Sutherland WJ, Pullin AS, Dolman PM, Knight TM (2004) The need for evidence-based conservation. Trends Ecol Evol 19:305–308. https://doi.org/10.1016/j.tree.2004.03.018

Sutherland CS, Elston DA, Lambin X (2012) Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. Ecology 93:2465–2473

Sutherland CS, Elston DA, Lambin X (2014) A demographic, spatialy explicit patch occupancy model of metapopulation dynamics and persistence. Ecology 95:3149–3160

Telfer S, Piertney SB, Dallas JF et al (2003) Parentage assignment detects frequent and large-scale dispersal in water voles. Mol Ecol 12:1939–1949. https://doi.org/10.1046/j.1365-294X.2003.01859.x

Trakhtenbrot A, Nathan R, Perry G, Richardson DM (2005) The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11:173–181. https://doi.org/10.1111/j.1366-9516.2005.00156.x

van der Vaart E, Johnston ASA, Sibly RM (2016) Predicting how many animals will be where: how to build, calibrate and evaluate individual-based models. Ecol Modell 326:113–123. https://doi.org/10.1016/j.ecolmodel.2015.08.012

Vasudev D, Fletcher RJ, Goswami VR, Krishnadas M (2015) From dispersal constraints to landscape connectivity: lessons from species distribution modeling. Ecography (Cop) 38:967–978. https://doi.org/10.1111/ecog.01306

Vatka E, Orell M, RytkÖNen S (2011) Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. Glob Chang Biol 17:3002–3009. https://doi.org/10.1111/j.1365-2486.2011.02430.x

Vörösmarty CJ, McIntyre PB, Gessner MO et al (2010) Global threats to human water security and river biodiversity. Nature 467:555–561. https://doi.org/10.1038/nature09440

Watling JI, Donnelly MA (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conserv Biol 20:1016–1025. https://doi.org/10.1111/j.1523-1739.2006.00482.x

Wiegand T, Knauer F, Kaczensky P, Naves J (2004) Expansion of brown bears (*Ursus arctos*) into the eastern alps: a spatially explicit population maodel. Biodivers Conserv 13:79–114

Williams P, Whitfield M, Biggs J (2008) How can we make new ponds biodiverse? A case study monitored over 7 years. Hydrobiologia 597:137–148. https://doi.org/10.1007/s10750-007-9224-9

Ziółkowska E, Perzanowski K, Bleyhl B et al (2016) Understanding unexpected reintroduction outcomes: why aren't European bison colonizing suitable habitat in the Carpathians? Biol Conserv 195:106–117. https://doi.org/10.1016/j.biocon.2015.12.032

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