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ORIGINAL PAPER

Impacts of habitat heterogeneity on the provision of multiple ecosystem services in a temperate floodplain

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Abstract

The relationships between habitat heterogeneity and the provision of multiple ecosystem services are not well understood. This study investigates the impacts of heterogeneity in surface floodwater inundation on the productive efficiency of ecosystem service provision, and the degree to which the relative provision of these ecosystem services is evenly balanced. We analyse indicators of five services. Field data from 100 floodplain quadrats were first analysed to investigate relationships between ecosystem service indicators and floodplain hydrology. Floodplain mosaics of varying hydrological heterogeneity were then simulated using the empirical data. Simulated floodplains with higher hydrological heterogeneity were generally less efficient in providing the target indicators, because they were adapted to the particular hydrological ranges which best provided the target services. Simulated floodplains that were more heterogeneous generally provided more even levels of the target indicators by segregating provision into different habitat types. Heterogeneity in floodplain hydrology may help to balance provision of multiple ecosystem services. However, management of hydrological heterogeneity to achieve this requires a detailed understanding of the relationships between each service and habitat conditions.

Keywords: Productive efficiency; Wetland restoration; Trade-off

Introduction

Heterogeneity in habitat conditions is an ecologically important characteristic of aquatic and wetland environments (Ward, Tockner, & Schiemer 1999; Palmer, Menninger, & Bernhardt 2010). For example, wetlands that are hydrologically more heterogeneous typically support higher species richness (Vivian-Smith 1997; Brose 2008), and habitat heterogeneity also enhances biodiversity in rivers (Vinson & Hawkins 1998). An understanding of the relationships between habitat heterogeneity and biodiversity is commonly used to inform biodiversity conservation in floodplain wetlands (Ward et al. 1999; Tockner et al. 1999) and river channels (Palmer et al. 2010; Gilvear, Spray, & Casas-Mulet 2013). It can be expected that hydrological heterogeneity will also have implications for ecosystem service provision, because the environmental conditions and ecological communities present in a wetland affect the ecosystem services

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(ES) that it provides to people (Morris, Posthumus, Hess, Gowing, & Rouquette 2009). However, we lack an understanding of the relationships between habitat heterogeneity and the provision of multiple ES (Bennett et al. 2015). The aim of this study is to investigate the impacts of hydrological heterogeneity on the evenness and efficiency of five indicators of floodplain ES.

Wetlands provide a range of benefits to people, including provisioning, regulating, and cultural ES (Zedler & Kercher 2005; Maltby & Acreman 2011). The provision of a particular ES is highest under specific physical and ecological conditions, so there are commonly indirect trade-offs between ES with conflicting requirements (Rodríguez et al. 2006; Bennett, Peterson, & Gordon 2009). The way in which multiple ES are provided at a particular wetland can be characterised according to two criteria: the degree to which the provision of multiple services is evenly balanced, and the overall efficiency of ES provision.

The efficiency of ES provision is defined here as productive efficiency, a metric that is commonly applied to multiple-criteria decision problems in engineering (Ngatchou, Zarei, & El-Sharkawi 2005), and has been used more recently to identify trade-offs in ES case studies (Sanon, Hein, Douven, & Winkler 2012; Lautenbach, Volk, Strauch, Whittaker, & Seppelt 2013). The environmental conditions in an area of habitat can be altered to change the ES that it provides, so different combinations of habitat conditions may provide different suites of ES. A habitat that provides a productively efficient suite of ES is one in which it is not possible to increase the provision of any ES without simultaneously degrading the provision of another (Lautenbach et al. 2013; Sanon et al. 2012). Productively efficient scenarios are identified by comparing the range of possible service provision outcomes against each other. The range of possible outcomes makes up a "decision space" (Reed, Hadka, Herman, Kasprzyk, & Kollat 2013), which can be visualised in cases of two ES by plotting the predicted value of the first service for each scenario against the predicted value of the second service (Fig. 1). Efficient ES outcomes are those that provide the maximum possible level of one service for a given level of the other; in graphical terms, the most efficient scenarios will form the boundary of the decision space which is closest to the top right corner (black dashed line in Fig. 1). This boundary is termed the "production-possibility frontier", and the ES scenarios that lie away from this frontier (e.g. the open circles in Fig. 1) are technically inefficient because there are alternative scenarios on the production-possibility frontier that could provide a higher level of Service 1 without degrading Service 2, or vice versa. The distance between a point in the decision space (representing the outcome of a scenario) and the production-possibility frontier can be used as an index of relative efficiency (Shaw 2012).

In addition to managing habitats to give productive efficiency, there is increasing interest in managing habitats to provide multiple ES evenly, rather than focusing on a single service (Wiggering et al. 2006). In some situations, it is desirable to provide an even balance of multiple ES because, in a specific location, the loss of a particular service may have substantial negative consequences that are not outweighed by the maximisation of others (Rouquette et al. 2011). Evenness of ES provision is quantified here as Pielou's J' (Pielou 1966). Scenarios that provide even levels of two ES lie away from the axes in Fig. 1 (Otte, Simmering, & Wolters 2007). The large black circle in Fig. 1 indicates the most even scenario of those that are also efficient. ES efficiency and evenness are therefore not mutually exclusive.

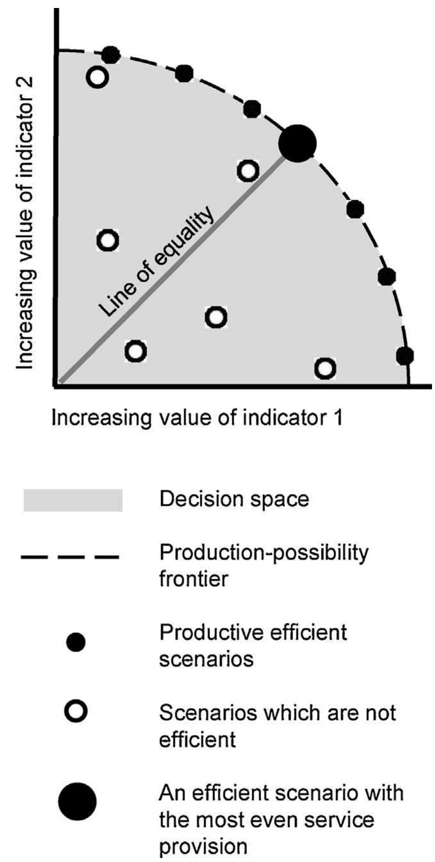

Fig. 1. Conceptual diagram indicating a trade-off between two indicators. The decision space of possible management outcomes is shown, bounded by the production-possibility frontier. Service provision is more efficient for scenarios that are closer to the production-possibility frontier and is increasingly evenly balanced for scenarios that are closer to the line of equality.

The provision of ES in lowland river floodplains is closely linked to the hydrological conditions that are present (Morris et al. 2009; Rouquette et al. 2011), and heterogeneity in hydrological conditions is a characteristic feature of floodplains that can be altered by habitat management practices (Ward et al. 1999). Previous studies that have aimed to inform specific management decisions have quantified relevant ES and developed contrasting potential scenarios representing different decisions. The present study takes a more general approach by comparing a characteristic of habitat structure (hydrological heterogeneity) to two attributes of a suite of ES

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(efficiency and evenness) that may be considered important by managers.

In this study, we investigate how hydrological heterogeneity can impact the efficiency and evenness of provision of ES indicators in a lowland river floodplain system. The objectives of the study are (1) to quantify the relationships between flood inundation and ES indicators, (2) to analyse the relationships between hydrological heterogeneity and the productive efficiency of ES provision, and (3) to analyse the relationships between hydrological heterogeneity and the evenness of ES provision. We quantified indicators of food provision (cattle grazing), aesthetics (wetland bird, and odonate presence), and plant biodiversity (the number of plant species of conservation significance that were present, and the proportion of the plant species present that were indicators of floodplain grazing marsh habitat). To analyse the impacts of hydrological heterogeneity on these five indicators we performed a series of resampling simulations that iteratively combined the sampled habitat patches to form larger mosaics. Analyses of hydrological heterogeneity were performed at two levels of complexity; pairwise for each pair of the five indicators, and for all five indicators together.

Materials and methods

Study site and selection of indicators

Indicators of floodplain quality were sampled across a gradient of flood exposure at a periodically inundated floodplain of the River Don, at Fishlake in the United Kingdom (Latitude: 53.611239, Longitude: −1.002889). Wetlands at the study site were drained in the 1600s and the river was embanked. The site has been used as a flood storage area and for cattle grazing since the 1940s (flooding on average twice per year). Similar fragments of land caught between flood defences and used for flood storage are relatively common in the area, which has been heavily drained and modified. However, the site is unusual in its more recent management; breaches were made in the river embankments in 2009 to allow more frequent inundation (approximately 130 flood events per year, to a varying degree on each occasion), and there is now considerable spatial variation in flood exposure due to differences in topography. Throughout this change in site management, the frequency of flooding across the floodplain was manipulated by altering the height of the flood defence bank breaches, and by sculpting the micro-topography within the floodplain (Richards 2014). The primary aim of the change made in 2009 was to restore floodplain habitats, and consequently the plant biodiversity that is characteristic of such systems. However, the site supplies various ES that may have been affected differently by the increased inundation. In addition to being used for grazing beef cattle, the area is publicly accessible and includes a public footpath. The site is used regularly by local visitors for recreation, including bird watching (Richards 2014). The Fishlake floodplain therefore provides an opportunity to analyse the relationships between hydrological habitat conditions and the provision of multiple ES.

Relationships between flood inundation and ES indicators

One hundred quadrats, each 20 m × 20 m in size, were sampled for five indicators. Five indicators of ecosystem services and biodiversity were identified following the typology used in the Millennium Ecosystem Assessment (MA, 2005). Two indicators of aesthetic ecosystem services were quantified; the presence of wetland birds, and the presence of odonates. One indicator of a provisioning ecosystem service was quantified; the presence of cattle dung. Two plant biodiversity indicators were also quantified; the similarity of the plant community to floodplain grazing marsh (FGM similarity), and the number of local Biodiversity Action Plan species (BAP species richness). In general terms, the five indicators were chosen because they are of greatest interest to the landowner; the national Environment Agency. As the agency responsible for environmental protection and enhancement, floodplain plant biodiversity is of particular interest (Richards 2014). Furthermore, the agency wishes to encourage public use of the site, as well as protect the livelihood of the tenant farmer (Richards 2014). The rationale behind each indicator and method of measurement is explained in detail below. Five additional environmental variables were also recorded; flood exposure, slope, altitude, and vegetation height. The quadrats were selected from a grid by random stratified sampling. There were four equally-sized strata across a gradient of flood exposure, from areas that were permanently flooded to those that were almost permanently unflooded.

Aesthetic ES: Two taxa that contribute positively to the aesthetic experience of visitors to the site were quantified as ecosystem service indicators. Odonates and wetland birds can have positive impacts on recreational experiences (Lemelin 2009; Green & Elmberg 2013). The study site is publicly accessible, and public preferences for odonates have been quantified at the study site (Richards, Warren, Moggridge, & Maltby 2015). The abundance of odonates was recorded following a three-minute search period within each quadrat. Each quadrat was surveyed in fair weather conditions during the odonate active season; three times in August 2012, and a further three times in August 2013. The activity of wetland bird species (*Cygnus olor, Anas platyrhynchos, Aythya fuligula, Ardea cinerea, Vanellus vanellus, Fulica atra, Tadorna tadorna, Anas strepera, Haematopus ostralegus, Anser anser, Anas crecca, Anas clyptea*) was recorded within each quadrat on six occasions in June 2012, and on a further six occasions between May and June 2013. Quadrats were viewed by two observers for 5 min from a raised flood bank running parallel to the site, at a distance of less than 100 m. Surveys were conducted between 7 and 10 am under fair weather conditions. The proportion of the 12 visits when wetland birds were encountered within a quadrat provides an index of habitat preference, but also a tangible recreational ecosystem service indicator; the probability of a visitor observing a wetland bird during a visit.

Provisioning ES: Cattle production has been an important use of the Fishlake floodplain for at least 70 years, with around 60 beef cattle grazing the site between April and November (Richards 2014). The presence of cattle dung in a quadrat was used to indicate the utility of the habitat for beef production, as dung is distributed in proportion to the time that cattle spend in an area (Jansen & Roberston 2001). This simplified metric of cattle use does not capture the total productivity of land for cattle farming (Morris & Brewin 2013), but provides a relative indicator over a short time period. Quadrats were searched for dung on two occasions in periods when cattle were known to be active on the site, once in July 2012 and once in April 2013. Major flooding of the site had not occurred for at least three weeks before the dung surveys.

Biodiversity: Plant biodiversity was categorised as an ecosystem service in this study because species and communities have an intrinsic cultural value (Chapin et al. 2000) which has been recognised through legislation or guidance; in this case through regional species action plans and national priority habitat status (Natural England 2013). Plant communities in each quadrat were surveyed in June or July in 2012 to make identification more straightforward due to flowering. All higher plant taxa, and filamentous algae, present within each quadrat were identified and assigned a frequency score on the DAFOR scale (Brodie 1985). Taxa were identified to species level except in the case of the grasses *Agrostis* and *Poa*, and filamentous algae were additionally classified as a group. Two indicators of biodiversity value were calculated for each plant community. The value of each plant community in contributing to the biodiversity of the region was quantified as the number of plant species that were present that were listed on the Local Authority biodiversity action plan (henceforth, BAP species richness). The value of each plant community in contributing to national biodiversity was quantified as its similarity to a nationally important habitat type; floodplain grazing marsh. Floodplain grazing marshes are a United Kingdom biodiversity action plan priority habitat (Mountford et al. 2006), and there is government and practitioner interest in conserving and restoring these communities (Mountford et al. 2006). Similarity to floodplain grazing marsh was defined as the proportion of floodplain grazing marsh species present in a sampled community (henceforth, FGM similarity). Floodplain grazing marsh species were defined as any species listed as occurring in the National Vegetation Classification communities (Rodwell 1991; Rodwell 1992) that were defined as floodplain grazing marsh by Mountford et al. (2006) (see Appendix A: Table 1 for a list of BAP and FGM species).

Environmental data were collected to model the provision of ecosystem service indicators. Hydrological conditions were measured as the frequency of flood inundation. An index of flood exposure was mapped continuously across the floodplain at a high resolution (scale: 1 pixel = 0.0625 m^2) as the number of hydrological survey dates that the area was underwater (minimum possible score = 0, maximum possible score = 52), using the methodology described in Richards (2014). In brief, the method used a field survey with handheld global positioning system to map the spatial extent of the surface water, and cross-referenced this extent with a high-resolution digital surface model to estimate the water level in different areas. The mean flood exposure score over the 52 survey visits within each quadrat was then calculated. Frequency of flood inundation is an incomplete indicator of hydrological conditions, as groundwater level and soil moisture also influence ecological conditions (Wheeler, Gowing, Shaw, Mountford, & Money 2004). Frequency of flood inundation was chosen as the indicator of floodplain hydrology because these data were available across the whole site, and because this hydrological parameter has been targeted by historical and current management practices Richards (2014).

Vegetation height within each quadrat was quantified as the mean of five measurements (one at each corner and the centre), which were taken in June 2012 using the method of Stammel, Kiehl, and Pfadenhauer (2003). The mean slope within each quadrat, and the mean elevation, were calculated directly from the topographic data described in Richards (2014).

Each ES indicator was modelled using regression in response to flood exposure and additional explanatory variables that could be expected a priori to be relevant. Floodplain grazing marsh similarity and BAP species richness were modelled in response to flood exposure and cattle dung density, because of the potential importance of grazing and hydrology in impacting community composition (Mountford et al. 2006). The presence of cattle dung was modelled in response to flood exposure and slope due to the potential impacts of these factors on cattle locomotion and habitat preferences (Ballard & Krueger 2005; Buss, Grassmaster, Shannon, & Simpson 2012). The presence of odonates and wetland birds was modelled in response to flood exposure and vegetation height, because these factors may impact habitat preferences (Everard & Noble 2008; Richards et al. 2015).

Binomial generalised linear models (GLMs) were used to model the proportion of floodplain grazing marsh species that were present, and the proportional occurrence of cattle dung, odonates, and wetland birds. A poisson GLM was used to model the number of plant BAP species that were present. Binomial regression is appropriate to model binomial probabilities, while poisson regression is appropriate to model count data (Crawley, 2014). The presence of quadratic relationships between flood exposure and all indicators was tested prior to building the maximal models. Quadratic terms were used in the maximal models if the quadratic flood exposure model had a lower Akaike's Information Criterion (AIC) score than the simple flood exposure model.

There was potential for spatial autocorrelation in all indicator datasets, so spatial eigenvector mapping was used to

Table 1. Sampling details for the five indicators at the quadrat and simulated floodplain scales.

Quadrat-level indicator	Floodplain benefit provided	Sampling method at field quadrats	Indicator used for simulated floodplains
Wetland bird presence	Aesthetic	Probability of occurrence recorded over 12 occasions	Probability of seeing a wetland bird at any quadrat in the simulated floodplain
Odonate presence	Aesthetic	Probability of occurrence recorded over six occasions	Mean odonate abundance over simulated floodplain
Cattle dung presence	Production of cattle	Probability of cattle dung occurrence recorded over two occasions	Proportion of sample quadrats with dung present
Number of BAP species present	Local biodiversity target	Sampled in June–July 2012. Number of BAP species present	Number of Biodiversity Action Plan (BAP) plant species present in simulated floodplain
Floodplain grazing marsh similarity	National biodiversity target	Sampled in June–July 2012. Proportion of species listed as floodplain grazing marsh indicators	Proportion of floodplain grazing marsh species present across simulated floodplain

create spatial predictor variables that were then included in the models. We used the data-driven approach proposed by Dray, Legendre, and Peres-Neto (2006) to define truncated connectivity matrices based on Euclidean distance for each service indicator separately. Moran eigenvector filtering for the connectivity matrix was then applied to the maximal regression model for each service indicator, to select a subset of spatial eigenvectors that removed significant autocorrelation from the model residuals. The selected eigenvectors were then added to the maximal model, and this model was simplified using a backwards stepwise procedure using AIC as the simplification criterion (Dray et al. 2006). Map processing was conducted using the sp and raster packages for R (Bivand, Pebesma, & Gomez-Rubio 2008; Hijmans & van Etten 2012), and spatial eigenvector mapping was conducted using the spdep package (Bivand 2013).

Relationships between hydrological heterogeneity and the productive efficiency of ES provision

Hydrological heterogeneity was quantified as the number of different hydrological habitat types that were present (i.e. habitat richness). To investigate the impacts of hydrological heterogeneity on ES provision from floodplain mosaics, we simulated a range of hypothetical floodplain scenarios. In each comparison of multiple ES indicators, a range of hypothetical floodplain mosaics were simulated and made iteratively more efficient to identify the limits of the decision space and define the production-possibility frontier.

Floodplain mosaics were simulated using a resample-with-replacement procedure (Edgington 1995). Groups of 10 survey quadrats were randomly sampled with replacement from the 100 available, and combined to create simulated floodplains of 0.004 km^2 in area. The value of the five indicators was then quantified for the simulated floodplain, slightly differently at this larger spatial scale than for the quadrat-scale statistical modelling of field data (Table 1). The differences in quantification between scales reflect the way that the ES are delivered to people; for example, wetland birds are visible from distance so it is assumed that a visitor will view them if they are present anywhere in the floodplain. In contrast, odonates are only visible from distances of less than 20 m (Richards et al. 2015), so the abundance of odonates is used as a proxy for the probability that they will be encountered.

The heterogeneity of simulated floodplains was quantified as the number of different hydrological habitat types that were present (i.e. habitat richness). Habitat types were defined by categorising the gradient of flood exposure into 52 equal-sized groups, based on the 52 survey visits that were made to map the flood extent. The relationships between hydrological heterogeneity and the relative efficiency of simulated floodplains were analysed as Spearman's rank correlation coefficient (ρ). The relationships between the hydrological heterogeneity and the evenness (J) of the efficient simulated floodplains were also compared using Spearman's ρ.

Productive efficiency can be calculated for any number of ES dimensions (Ngatchou et al. 2005). We analysed efficiency at two levels of complexity; pairwise for each pair of the five ES indicators, and in relation to all five indicators together. The efficient simulated floodplains were found for each pair of the five indicators separately using an iterative process. For each pair of indicators, a starting population of 1,000,000 simulated floodplains was randomly generated, and the production-possibility frontier for this starting population was calculated. The simulated floodplains that fell on this frontier were then randomly modified to form a second generation of 300,000 simulated floodplains. During each random modification event, a random number of patches in the simulated floodplain were replaced with patches that were sampled randomly from the pool of 100 survey quadrats. This

Table 2. Summary of regression models developed for each ES indicator at the quadrat scale. Explanatory variables that were retained in each final model following simplification by AIC are shown, with an indication of the statistical significance of their coefficient. Increasing numbers of asterisks (*, **, ***) indicate the statistical significance of the coefficient at the $p < 0.05$, $p < 0.01$, and $p < 0.001$ levels respectively. For full details of the regression models including coefficient values and precise statistical significance, see Tables S2–6.

ES indicator	Explanatory variables in the final model and significance level
Floodplain grazing marsh similarity	Flood exposure**
Number of BAP species present	Flood exposure***
Cattle dung presence	Flood exposure***
Odonate presence	Flood exposure*** + flood exposure squared*** + vegetation height + spatial predictor***
Wetland bird presence	Flood exposure*** + flood exposure squared*** + vegetation height*

process was repeated until the frontier stabilised, and after each iteration a random subset of the simulated floodplains in the decision space was recorded for further analysis. In addition to the 10 pairwise analysis, a similar iterative process was carried out for all five indicators together, the only difference being that this analysis used generation sizes of 1,000,000 simulated floodplains. The iterative analyses of efficiency were conducted in R, using a reimplementation of routines for production-possibility frontier calculation that was originally written in Python (Bull 2012).

As a by-product of the efficiency analyses, a range of inefficient floodplains were simulated within the decision spaces. The relative efficiency of each simulated floodplain was quantified as the inverse of the minimum normalised Pythagorean distance from the production-possibility frontier.

It was not possible to assess the significance of the correlations between heterogeneity and efficiency because the sample size, and therefore the number of degrees of freedom, was arbitrary as a result of the simulation method. However, the simulated floodplains used in the analyses are a subset of the decision space that was sampled following an extensive, iterative procedure that searched millions of possibilities. The subset used in the correlations is therefore highly likely to represent the simulation system well.

Relationships between hydrological heterogeneity and the evenness of ES provision

When analysing the evenness of ES provision, we analysed only the simulated floodplains that were on the frontier, so as to hold the efficiency of provision constant and thus control for this factor. The evenness of the efficient simulated floodplains on the production-possibility frontier was quantified as the evenness (Pielou's J'; Pielou 1966) of the suite of indicators, with each service indicator normalised as the proportion of the maximum value encountered on the frontier.

Statistical significance cannot be assessed for the correlations between heterogeneity and evenness because the sample size was often small, as it depended on the number of simulated floodplains that made up the production-possibility frontier. Confidence in the hydrological heterogeneity vs. ES evenness correlations is increased because although these analyses used small sample sizes, the floodplains used in the analyses were all efficient in providing ES, thus minimising any confounding variation due to differences in their level of efficiency.

Results

All indicators responded significantly to the hydrological gradient (Table 2) and indicative relationships between flood exposure and each service indicator are shown in Fig. 2. Flood exposure was a significant predictor of all indicators (Table 2; for full details of the regression models see Appendix A: Tables 2–6). The proportion of FGM plant species in the community, the number of BAP plant species present within a quadrat, and the probability of cattle dung presence decreased significantly with increasing flood exposure (Table 2; Fig. 2A–C). The probability of sighting odonates and wetland birds had significant unimodal responses to flood exposure (Table 2; Fig. 2D and E), with peak values at flood exposures of 40 and 38 flooded occasions respectively (Fig. 2D and E).

When analysing the relationships between pairs of indicators at the scale of simulated floodplains, production-possibility frontiers were found in eight of the ten cases (Fig. 3A–H) indicating that there was some level of trade-off between the provision of these pairs of ES. Two pairs of indicators were synergistic, meaning that there were simulated floodplain configurations that allowed the provision of both ES to be maximised together. These two pairs of indicators were FGM similarity and cattle suitability (Fig. 3I) and wetland bird presence and BAP species richness (Fig. 3J).

There was a negative correlation between hydrological heterogeneity and the relative efficiency of provision in nine of the ten pairwise comparisons (Table 3). In the synergistic relationship between the probability of wetland bird presence and BAP species richness, scenarios that were more efficient were also more heterogeneous, although this effect was relatively weak (Table 3). In the case where production efficiencies were calculated for providing all five ES together, floodplains that were more heterogeneous were also less efficient at providing multiple service indicators (Table 3).

The relationships between hydrological heterogeneity and evenness were compared for the simulated floodplains on the

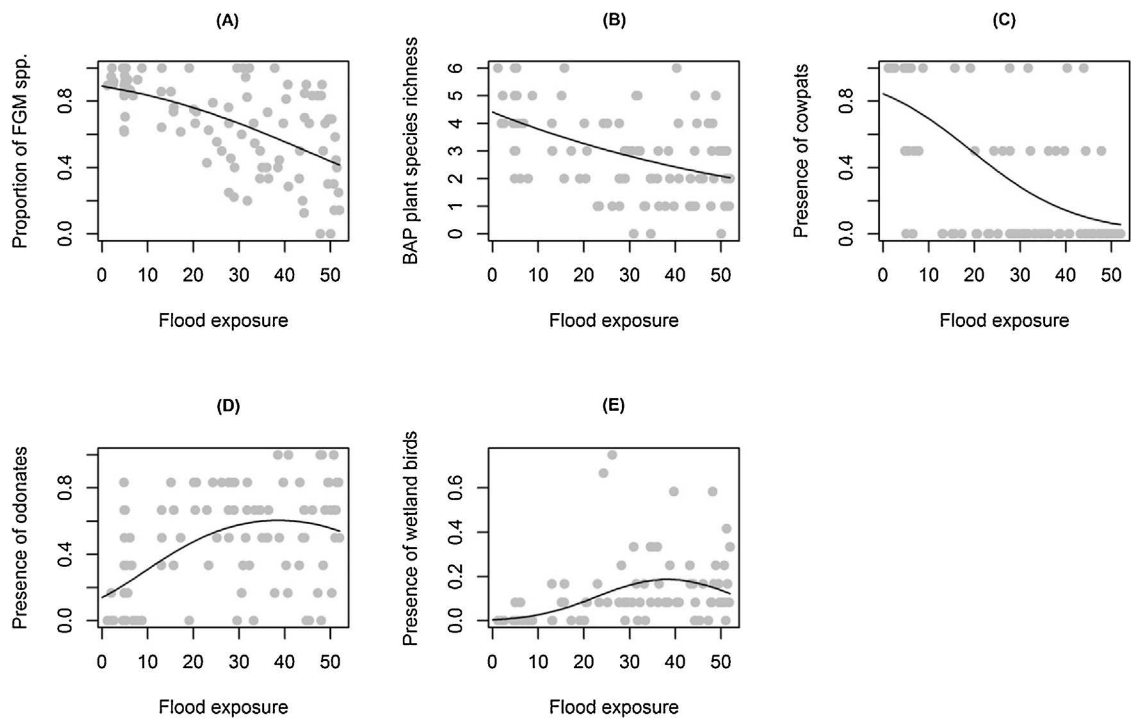

Fig. 2. Indicative relationships between five ES indicators and flood exposure (the mean number of 52 survey occasions when the areas within the quadrat were flooded). Black fitted lines in these figures correspond to the response variable modelled as a function of flood exposure only, rather than the more complex models described in Tables S2:S6. This is because it would be complex to interpret figures in which the dimensionless spatial eigenvector values included in the full models were held constant. Figures (D) and (E) model flood exposure as a second degree polynomial.

Table 3. Relationships between habitat heterogeneity and the efficiency and evenness of a suite of five indicators. Evenness is analysed across productive-possibility frontiers only. Figure numbers correspond to the trade-off plots shown in Fig. 3. Floodplain grazing marsh (FGM) similarity and Biodiversity Action Plan (BAP) species richness are abbreviated.

Figure number	Service indicator 1	Service indicator 2	Correlation between heterogeneity and efficiency (Spearman's ρ)	Correlation between heterogeneity and evenness (Spearman's ρ)
3A	FGM similarity	Odonate abundance	−0.85	0.39
3B	FGM similarity	BAP species richness	−0.36	0.95
3C	FGM similarity	Wetland bird probability	−0.30	0.99
3D	BAP species richness	Cattle suitability	−0.25	0.76
3E	BAP species richness	Odonate abundance	−0.71	0.68
3F	Cattle suitability	Odonate abundance	−0.82	0.67
3G	Cattle suitability	Wetland bird probability	−0.40	0.99
3H	Odonate abundance	Wetland bird probability	−0.64	0.55
3I	FGM similarity	Cattle suitability	−0.49	No frontier
3J	BAP species richness	Wetland bird probability	0.19	No frontier
No figure	Efficiency of all five indicators analysed together		−0.43	0.53

production-possibility frontier, for the eight applicable pairs of ES indicators (i.e. excluding the two synergistic relationships). All pairs of indicators showed a positive correlation between hydrological heterogeneity and evenness (Table 3). In the case where productive efficiencies were calculated for providing all five indicators together, more heterogeneous floodplains provided the five indicators more evenly (Table 3).

Discussion

Hydrology determines trade-offs between floodplain ES

Hydrology has a strong influence on the ES that a patch of floodplain provides (Morris et al. 2009), and the indicators in this study showed one of two types of relationships with

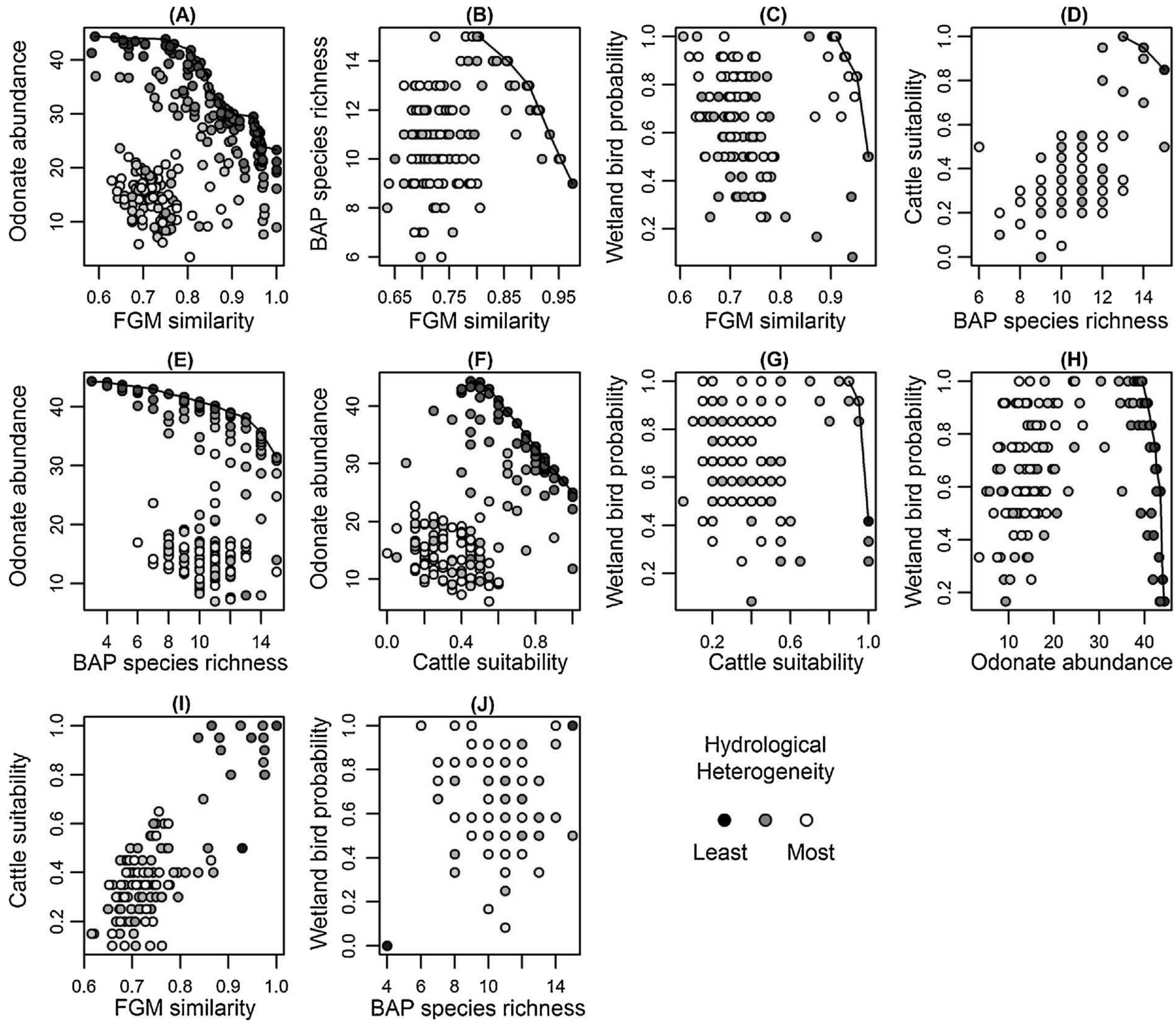

Fig. 3. Pairwise trade-off or synergy relationships between the provision of five indicators in simulated floodplains. Each point represents a simulated floodplain, coloured by the number of hydrological habitat types present within it. Higher values for all indicators are desirable, so in each case the ideal efficient and even solution would be in the top right corner. In each relationship production-possibility frontiers are marked by black lines, if applicable. Heterogeneity is coloured on a greyscale spectrum. More heterogeneous simulated floodplains are coloured white, while the least heterogeneous simulated floodplains are black.

hydrology. Less frequently flooded quadrats benefited the two plant biodiversity indicators because they provided suitable habitat for greater numbers of wet grassland plant species, many of which were either distinctive of floodplain grazing marshes or listed on the local Biodiversity Action Plan, or both. Less frequently flooded quadrats were also preferred by cattle, probably because grassland vegetation is more palatable (Buss et al. 2012), and locomotion in wetter environments is more difficult and hazardous (Ballard & Krueger 2005). On the other hand, more frequently flooded areas provided more suitable habitats for wetland birds and odonates (Everard & Noble 2008); taxa which are of recreational interest (Green & Elmberg 2013; Richards et al. 2015). The wettest quadrats provided lower quality habitats for birds and odonates, probably because these quadrats did not contain the adjacent bankside habitat and tall vegetation that these taxa require (Everard & Noble 2008; Richards et al. 2015). Trade-offs between ES indicators were largely indirect as they were driven by hydrological requirements of each indicator, but direct interactions between the factors, such as cattle grazing impacts on plant and animal communities, may strengthen these relationships through direct mechanisms (Bennett et al. 2009).

Hydrological heterogeneity impacts the efficiency and evenness of ES provision

The hydrological heterogeneity of the simulated floodplains affected the efficiency of ES indicators because of the underlying relationships between flood exposure and the provision of individual indicators. Different habitat patches varied in the contribution that they made to the indicator

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provision of a simulated floodplain, and some patches were superior to others in the context of each set of target indicators. Highly heterogeneous simulated floodplains tended to be less efficient because, by chance, they contained greater numbers of patches that were poor at providing the target indicators. More efficient simulated floodplains contained greater numbers of patches that were good at providing the target indicators, and because the indicators responded to hydrology, these patches often had similar or identical flood exposures. The most efficient floodplains were thus more hydrologically homogenous because they were more specialised to provide their target indicators. Similar patterns are observed in intensive agricultural landscapes, which are commonly homogenous because they are highly specialised to provide particular (agricultural) ES (Roschewitz, Thies, & Tscharntke 2005). The observed negative relationship between hydrological heterogeneity and ES indicator efficiency is likely to be general to other wetland habitats, because the provision of most ES requires specific environmental conditions (Maskell et al. 2013), and is enhanced when there is a greater area of suitable habitat (Barbier et al. 2008; Smukler et al. 2010). In the present study, the strength of the negative relationship between heterogeneity and efficiency for the case of all five ES indicators was intermediate to those of the 10 pairwise analyses. However, if a larger number of target ES were considered then hydrological heterogeneity may be expected to have a weaker negative effect on efficiency. When considering a larger number of target ES, it is likely that a broader range of hydrological conditions will provide some efficiency benefit, so floodplain mosaics that are less hydrologically specialised can be productively efficient.

Hydrological heterogeneity had a negative impact on efficiency, but a positive effect on evenness of ES indicators. Among the efficient simulated floodplains, those that were more heterogeneous provided a more even balance of the target ES indicators. More heterogeneous simulated floodplains gave more even provision because patches with contrasting hydrological conditions provided different ES indicators; the production of different indicators was effectively segregated into different parts of the simulated floodplain (Mander, Helming, & Wiggering 2007). Evenness in provision may not always be enhanced by hydrological heterogeneity, for example, in cases where multiple ES require similar habitat conditions (i.e. synergies). However, heterogeneity is likely to result in more even ES provision in the majority of cases, where different ES require different habitat conditions and there are trade-offs in provision (Rodríguez et al. 2006; Bennett et al. 2009).

Efficiently providing an even balance of multiple ES

This study indicates that to improve the productive efficiency of ES provision it is important to understand the specific environmental conditions that each target service requires. It may be easier to provide efficient habitats that provide high levels of only one ES, because in these cases it is not necessary to understand any trade-offs between providing different ES. Efficient habitats that evenly balance the provision of multiple ES may be more complex to design because the habitat requirements, scaling relationships, and interactions between multiple ES must be known (Lovell & Johnston 2009). As an alternative to trying to guess the correct environmental conditions for efficient ES provision, adaptive management could be applied to fine-tune habitat management over time, to more efficiently provide multiple ES simultaneously (Folke, Hahn, Olsson, & Norberg 2005; Kremen 2005). Real-world habitat management is unlikely to target maximum evenness in ES provision, but will attempt to balance the provision of different ES in a way that is satisfactory to the relevant stakeholders (Ananda & Herath 2009). To that end, it is encouraging that some level of co-production of ES appears to be very common: even the simulated floodplains that were most specialised for the provision of one ES indicator provided some level of the other (Fig. 3). In some trade-offs, substantial levels of apparently conflicting service indicators could be provided together. For example, some efficient simulated floodplains were entirely suitable for cattle production, but also provided suitable habitat for odonates (Fig. 3F), despite the different hydrological requirements of these service indicators (Fig. 2C and D).

Previous studies that have aimed to inform specific management decisions, have quantified relevant ES and corresponding aspects of environmental conditions. The present study took a more general approach by comparing a non-specific characteristic of habitat structure (heterogeneity) to two attributes of a suite of ES (efficiency and evenness). The observed relationships between hydrological heterogeneity and the efficiency and evenness of ES provision are likely to be widely applicable in wetlands and other habitats where environmental conditions strongly influence ES provision. The observed relationships between hydrological heterogeneity and ES efficiency and evenness can be expected to hold across other similar situations, because the underlying mechanisms are likely to remain the same; individual ES are best provided under specific ranges of environmental and habitat conditions, ES provision commonly scales positively with increasing habitat area, and increasing the areal coverage of one habitat results in decreasing coverage of others.

Future applications of scenario generation: putting people into the model

This study compared patterns in the provision of ES indicators, but did not consider people's demand for different ES. Stakeholder preferences for ES are an important driving force in the design of habitat management, particularly in cases where participatory design has been encouraged through stakeholder outreach (D' Aquino, Le Page, Bousquet, & Bah 2003). Stakeholders in floodplain management do not only consider their relative preferences for ES, but also have opinions on their willingness to pay for floodplain management; in terms of time, financially, and in terms of uncertainty in the outcomes of management changes. The costs of the management scenarios simulated in the present study were not taken into account, as we focused on analysing supply-side efficiency of ES. To enhance the applicability of the simulation process for informing real-world management, people's preferences for ES, and the costs of management, could be incorporated into the simulation. When optimising production-possibility frontiers in relation to ES demand and management costs, the values of services could be weighted according to preferences elicited through stakeholder workshops or surveys (Sanon et al. 2012). Similarly, to deliver evenness of provision of the desired services, preference judgements could be used to identify thresholds of ES provision that would be required by the various stakeholder groups (Posthumus, Rouquette, Morris, Gowing, & Hess 2010). Through combining supply- and demand-side optimisation, simulation could identify management scenarios that would provide ES in a way that is both efficient and multifunctional.

We quantify the evenness of ES provision as an important characteristic to consider when designing floodplain management, because it has potential implications for balancing the needs of different stakeholders. However, it is complex to quantify evenness in ES provision given the different metrics and scales used to quantify contrasting ecosystem services. Our measure of ES provision evenness is therefore somewhat arbitrary. Conversion of all ES values to a common unit, such as an economic value, may help to better quantify evenness, although the process of such economic valuation is highly complex and may exacerbate uncertainty in the estimates of value (Chee 2004). An alternative way to consider evenness in provision would be to relate the supply of ES to the demand of the stakeholders; for example, by quantifying the extent to which different scenarios of supply "satisfy" stakeholder demand. Despite the challenge involved in measuring ES provision evenness, this study indicates that it may be more difficult to manage floodplains in order to deliver evenness, than to deliver just one ES efficiently.

The management of floodplain wetlands can be considered at a range of scales; from individual patches, to mosaics, to whole networks of wetlands that are connected by watercourse networks. The importance of managing floodplains to provide evenness of ES provision also changes with scale; if we only consider one site then it may be important to provide a range of services, while at a larger spatial scale it may be more efficient to segregate provision by specialising particular floodplains to provide a limited number of ES. Some sites have higher potential to provide some services than others, so specialisation of different floodplains may help when integrating the supply of ES with stakeholder demands for them, by providing people in different areas with the benefits that they value most highly.

This study analysed relationships between the heterogeneity of simulated floodplains and the suite of ES that they provide, but the spatial structure of floodplain mosaics is also likely to be important. Spatial structure is likely to have an impact on the ES provided, as some ES are affected by habitat connectivity (Mitchell, Bennett, & Gonzalez 2013), or require different kinds of habitat to be adjacent to each other. Investigation of the impacts of these aspects of habitat structure could reveal further relationships between the structure of habitats and their ES provision.

Conclusion

The provision of floodplain ES is affected by hydrological factors such as the frequency of flood inundation. This study has shown that heterogeneity in the surface inundation of a simulated floodplain has an impact on both the efficiency and evenness of its ES provision. Spatial heterogeneity in flood inundation frequency can allow notable levels of multiple ES indicators to be provided simultaneously, even when the different indicators require very different environmental conditions. The simulation approach presented here may allow decision makers to design floodplain management that delivers a chosen set of ecosystem services. However, to optimise the supply of floodplain ES in relation to the demand for them and costs of management, further information is required on these parameters. Future approaches may incorporate stakeholder preferences and knowledge to help select management options that are most suitable in a given situation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.02.012.

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