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Spatial covariance between biodiversity and other ecosystem service priorities

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Summary

1. Ecosystems support biodiversity and also provide goods and services that are beneficial to humans. The extent to which the locations that are most valuable for ecosystem services coincide with those that support the most biodiversity is of critical importance when designing conservation and land management strategies. There are, however, few studies on which to base any kind of conclusion about possible spatial patterns of association between ecosystem services and biodiversity. Moreover, little is known about the sensitivity of the conclusions to the quality of the data available, or to the choice and size of the region used for analysis.

2. Here, we first present national-scale estimates of the spatial covariance in areas important for ecosystem services and biodiversity (richness of species of conservation concern), using Britain as a case study. We then explore how these associations are sensitive to the spatial resolution of the available data, the spatial extent of our study region and to regional variation across the study area.

3. Our analyses reveal a mixture of negative and positive associations. In particular, the regionalization analysis shows that one can arrive at diametrically opposing conclusions about relationships between ecosystem services and biodiversity by studying the same question within different areas, even within a moderately small island.

4. *Synthesis and applications*. In a policy context, the location-specific nature of relationships between ecosystem services and biodiversity underscores the importance of multi-scale environmental decision-making, so as to reflect both local conditions and broader-scale priorities. The results also suggest that efforts to establish general patterns of congruence in ecosystem services and biodiversity may offer a less constructive way forward than do more regional approaches.

Key-words: agriculture value, BAP species, Britain, carbon storage, conservation, ecosystem services, planning, recreation, species richness, trade-offs

Introduction

The focus of conservation priorities and land use policies is broadening to recognize the variety of goods and services that people derive from ecosystems (Millennium Ecosystem Assessment 2005) as well as the needs of priority species and habitats (Armsworth *et al.* 2007; Daily & Matson 2008). The spatial overlap between habitats important for providing different ecosystem services and biodiversity benefits is of critical importance when designing conservation and land management strategies. Do those areas that serve as important stores of carbon also play a key role in supporting species of conservation concern? Can those same habitats meet the growing needs of agricultural production or demands from society for recreation and open space amenities? If so, then there are policy win-wins to be obtained. Policies and strategies introduced to safeguard the provision of one ecosystem service will yield ancillary benefits for others. Moreover, the potential benefits of habitat conservation have a greater chance of outweighing the economic gains to be had from habitat conversion when multiple services can be bundled together and provided by a single ecosystem (Balmford *et al.* 2002). On the other hand, if there is little overlap between habitats important for providing different ecosystem

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services and biodiversity benefits, then difficult trade-offs must be confronted. At best, a portfolio of bespoke conservation strategies will be needed to deliver the suite of benefits from ecosystems that society demands. And at worst, by focusing attention on some ecosystem services, the conservation and policy communities risk diverting limited resources away from habitats important for providing other benefits (McCauley 2006) or displacing development pressures on to them.

There are few studies on which to base conclusions about the spatial relationships between habitats important for different ecosystem services and benefits for biodiversity. Generally, such data are scarce, and so spatial correlations between ecosystem services have often been assumed rather than demonstrated (e.g. Troy & Wilson 2006; Turner *et al.* 2007). Notable examples of attempts to estimate the relevant spatial relationships include the Chan *et al.* (2006) study of the Central Coast ecoregion in California, which found only weak relationships between ecosystem services and biodiversity. More recently, Naidoo *et al.* (2008) correlated ecosystem service provision across ecoregions around the globe and also found only weak relationships between areas that were important for providing different services.

Little is known from the available studies about the sensitivity of their conclusions (about the spatial associations between ecosystem services and biodiversity) to the quality of the data available, or to the choice and size of the region chosen for analysis. However, when studying the contribution of different areas to supporting biodiversity, other authors have revealed a strong dependence of the results on all of these design elements. For example, Rahbek & Graves (2001) and Davies *et al.* (2007) showed that the relative importance of different environmental factors to avian richness patterns is sensitive to the spatial resolution of the data. Likewise, Rodrigues & Gaston (2002) showed that the apparent rarity of species depends on the size and choice of the study region in South African birds. Importantly, these data dependencies affect conservation priorities and land management strategies that one would ultimately recommend (resolution of data – Shriner, Wilson & Flather 2006; extent and regional variation – Rodrigues & Gaston 2002; Strange *et al.* 2006).

Here, we first present national-scale estimates of the spatial covariance in areas important for ecosystem services and biodiversity, using Britain as a case study. This is a region in which an ecosystem approach to land use planning is being widely discussed and promoted by governmental and non-governmental bodies (Sutherland *et al.* 2006). We then test the sensitivity of these estimates to the spatial resolution of the available data, the spatial extent of our study region and to regional variation across the study area. We assembled spatial surfaces of ecosystem service and biodiversity benefits at two resolutions (4 and 100 km^2) and two spatial extents (Britain/England and 100×100 km squares across Britain). Finally, taking the finest resolution and smallest spatial extent, we examined how the covariance structures varied across regions within Britain. For biodiversity we used the richness per unit area of 'species of conservation concern' (Biodiversity Action Plan species). These taxa are prioritized by the UK government for conservation (http://www.ukbap.org.uk/NewPriorityList.aspx). We considered three ecosystem services: (i) carbon storage (above ground and below ground to 1 m depth; in kg m^{-2}); (ii) agriculture value (in terms of annual income); and (iii) recreational use of the countryside (in terms of numbers of day visits, available for England only).

Materials and methods

DATA

Biodiversity

The UK Biodiversity Action Plan (UK BAP) lists species with priority for conservation action within the UK (http://www.ukbap.org.uk/NewPriorityList.aspx). These species are considered 'species of conservation concern' and have statutory protection. As such, they represent the element of biodiversity for which conservation targets are in place; and because of their priority status distribution data are likely to be more complete. Here we only consider species distributions within Britain, i.e. England, Scotland and Wales. As we are concerned with associations between biodiversity and terrestrial ecosystem services, marine species and fish were excluded, as were birds whose main feeding resources are marine. All non-marine feeding birds, terrestrial mammals, herptiles (amphibians and reptiles) and vascular plants were included, as were bryophytes and butterflies. Limited distribution data prevented us from including fungi, and other non-vascular plants and terrestrial invertebrates.

Bird records were supplied by the British Trust for Ornithology (BTO) and are the tetrad data on which the 1981–1991 New Atlas of breeding birds in Britain and Ireland is based (Gibbons, Reid & Chapman 1993). In order to standardize sampling effort, BTO made every effort to ensure that at least eight tetrads were surveyed within each 10×10 km British National Grid square. Where possible, tetrads were visited at least twice for 1 h each, in April to May and in June to July, although in some remote upland areas a single 2 h visit was made. Where eight or fewer tetrads were sampled (e.g. in partial 10×10 km squares) all available squares were used. Where more than eight tetrads were surveyed within a 10×10 km square, eight were chosen at random.

For bryophytes, vascular plants, butterflies, herptiles and mammals, all distribution records held by the Biological Records Centre, Centre for Ecology and Hydrology as of January 2008 were initially considered regardless of date of recording. Where these were recorded at finer resolution than the 2×2 km tetrad that the bird records were obtained at, the record was centred on the tetrad and all duplicate (same species and tetrad) records were removed. For comparability between resolutions biodiversity at the 10×10 km resolution was calculated only from the records used in the 2×2 km analysis (Fig. 1a). Records only available at coarser resolution were not used.

In order to make all the biodiversity data comparable, the 20 246 sampled tetrads were used as the template for all the 4 km^2 analyses (for all taxa). This may have led to some small bias towards tetrads likely to contain 'interesting' birds.

Carbon

We obtained vegetation carbon data at the 1×1 km grid resolution from the Centre for Ecology and Hydrology (Milne & Brown 1997); to make the data resolution comparable to that available for other ecosystem services and biodiversity, we aggregated the 1×1 km data

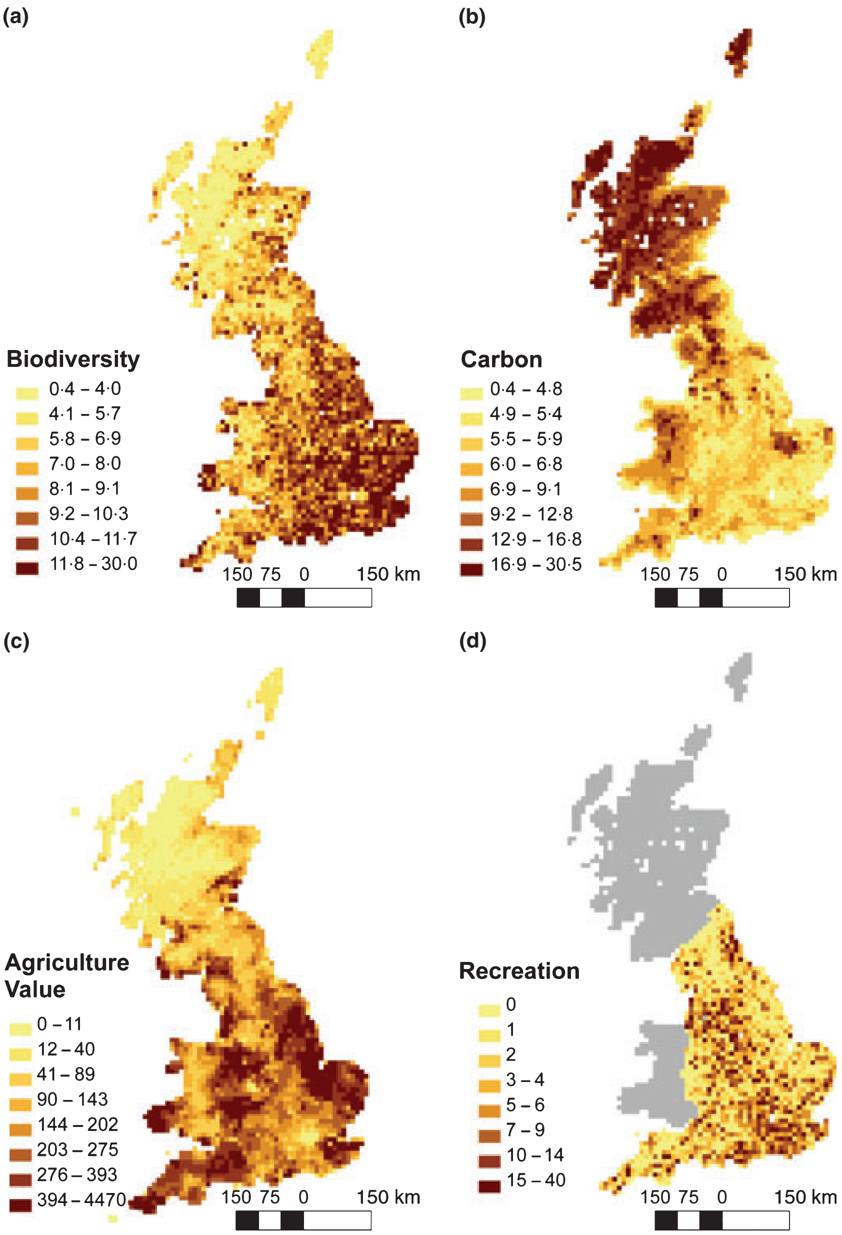

Fig. 1. Distribution of Biodiversity and Ecosystem Services within Britain. The distribution (at 100 km^2 resolution) of: (a) Biodiversity (mean number of species of Biodiversity Action Plan, priority species); (b) Carbon [above and below (to 1 m depth) ground, kgC m^{-2}]; and (c) Agriculture Value (£ sterling year^{-1} ha^{-1}), all based on the mean of the subsampled tetrads; (d) Recreation in England (number of rural outdoor visits, from ELVS sample) at 100 km^2 resolution.

to 2 × 2 km or 10 × 10 km grid squares (Fig. 1b). Soil parameter, land use and soil series data were obtained from the National Soil Resources Institute for the top 1 m of soil (to bedrock or 1 m depth, whichever was less) which enabled us to calculate soil carbon density at the 1 × 1 km grid resolution in two steps. First, we calculated the soil organic carbon density values for each of the 977 soil series in Britain based on their percent soil organic carbon, bulk density and stoniness. Second, we calculated the average soil organic carbon density per 1 × 1 km grid cell based on this soil series and land use data. The latter calculation was done as a weighted average based on the five dominant land uses (wood, semi-natural, grassland, arable and garden). Estimates for areas with no specified carbon content (towns, roads, etc. or soil series with unknown carbon content) were obtained from the area weighted average of specified carbon densities of land use and soil series combinations within each grid cell. We then calculated the total carbon per 1 × 1 km grid cell by adding the soil organic carbon and vegetation carbon grids together. This grid was then clipped to include only the land area of Britain.

Agriculture value

The agriculture value layer is the summed gross margin of all major crops, and livestock (Fig. 1c). It was calculated by multiplying the area of all major crops (or number of livestock) by the gross margin per unit area or livestock unit (gross margin = value of output − variable costs and subsidy payments). Raw yields in relevant units (e.g. tonnes ha^{-1}) were obtained from agricultural survey data (DEFRA 2005; Scottish Executive Environment and Rural Affairs Department 2006; Welsh Assembly Government 2006), and were converted to gross margins based on estimates from the Farm Management Handbook 2007/2008 (Beaton, Catto & Kerr 2007) (see Table S1 and Appendix S1 in Supporting Information).

Recreation

Our goal was to assess which portions of the countryside were most valuable for recreational use for the English population as a whole.

To achieve this we used a representative survey of leisure trips of the entire English population – the England Leisure Visits Survey 2005 (main survey) (http://www.countryside.gov.uk/Images/ELVS05_tripbased_revised_tcm2-31285.zip). More specifically, we considered the number of day leisure visits ($n = 6279$ for all of England) to rural locations (where the main purpose was enjoyment of the landscape) to be representative of the recreation value of the landscape. We considered walking, cycling, swimming, visiting a beach, playing sport, a rural hobby (e.g. fishing), visiting a rural attraction, park or garden, going for a drive in the countryside and relaxing in the countryside, all to constitute enjoyment of the landscape. Day leisure visits are defined as any round trip of less than 1 day in duration made from home (or a holiday destination in England) for leisure purposes (http://www.naturalengland.org.uk/Images/elvsbrochure_tcm6-4896.pdf).

ANALYSES

All statistical analyses were carried out in R 2·7 (R Development Core Team 2008), and all GIS analyses in ArcGIS/ArcInfo 9.2 (ESRI 2006). Spearman rank correlations were carried out for all associations as the distribution of the data are clearly not normal and transformations failed to correct this. In order to illustrate the associations, values of the variable on the x-axes of Fig. 2 (Biodiversity) and Fig. 3 (Carbon and Recreation) were grouped/binned into eight quantiles (the spatial distribution of these quantiles is shown in Fig. 1) and presented as box-plots. Correlations are based in all cases on the raw data.

Hotspots for biodiversity, carbon and agriculture value were calculated using three cut-off points, the top 10%, 20% and 30% of squares for each layer. Hotspots involving the Recreation layer were based on the top 10%, 20% and 30% of squares within England for each layer.

Results

Initial examination of the spatial surfaces of biodiversity and ecosystem services (Fig. 1) suggests that they are not congruent. The richness of species of conservation concern is concentrated in the south and east of Britain (Fig. 1a), whereas important carbon stores lie predominantly in the colder and wetter north and west, as well as in a few areas with lowland peat soils (Fig. 1b). High-value agriculture is mainly in the non-urban lowlands of the south (Fig. 1c). The recreation sample, available for England only, suggests peak activity in regions with high human population densities around London and the arc of conurbation that encompasses the cities of Manchester, Birmingham, Sheffield and Leeds (Fig. 1d).

Correlations between biodiversity and ecosystem services measured on 10 × 10 km squares reflect these patterns (Fig. 2) and this pattern is robust to the measure of biodiversity used (see Figs S1–S3, Supporting Information). Areas that are important stores of carbon support low biodiversity over national scales (Fig. 2a; Figs S1–S3). In contrast, agriculture value is positively associated with high biodiversity (Fig. 2c; Figs S1–S3) and there is no relationship between areas important for biodiversity and recreation in England (Fig. 2e; Figs S1–S3).

Turning to the relationships between the different ecosystem services themselves, carbon storage is, unsurprisingly, negatively correlated with agriculture value (Fig. 3a); high value farmland, in particular, was associated with low carbon, except for a few lowland areas on peat soils of importance to horticulture (Fig. 1). Recreation in England was weakly negatively correlated with both ecosystem carbon and agriculture value (Fig 3c,d), probably reflecting that human population densities are relatively low in regions with high carbon and high agricultural productivity.

When we examine the overlap of hotspots for biodiversity and ecosystem services, the evidence of spatial overlap at a 10 × 10 km resolution looks weaker (Table 1 and Table S2, Supporting Information). We compared the sets of grid squares identified as being among the top 10%, 20% and 30% of areas for providing each ecosystem service and biodiversity. The overlap between these sets was typically very poor. There was less than 4% overlap between the sets of 'hotspot' locations identified for all pairwise combinations of ecosystem services, and between biodiversity and carbon storage or recreation. The greatest overlap (up to 14% of the grid squares selected, depending on how strict a criterion defines a hotspot) came between locations important for biodiversity and high agriculture value, reflecting the strong positive relationship between these surfaces revealed in the correlation analysis (Table 1 and Table S2).

SPATIAL RESOLUTION OF THE DATA

The available data are such that we can test the sensitivity of our results to the resolution over which biodiversity data and data on carbon storage and agriculture value are available. We repeated all of the above analyses using data reported on a finer resolution 2 × 2 km square grid. Enhancing the resolution of the data in this way did not change the broad spatial covariance structures. Once again, carbon storage and agriculture value were respectively negatively and positively associated with biodiversity, and negatively associated with each other (Figs 2bd, 3b). Overlap of hotspot squares was still generally very poor, and greatest between locations that were most important for biodiversity and agriculture value (Table 1). In all cases, increasing the resolution of the data weakened the rank correlation estimates across all grid squares, but improved the percentage overlap of the highest value grid squares.

SPATIAL EXTENT OF THE DATA

We then tested the sensitivity of the spatial covariance structures to the spatial extent of the study area. Using the higher resolution data (2 × 2 km) we compared the correlations between biodiversity and ecosystem services within each of the 100 × 100 km British National Grid squares and for an identical number of 2 × 2 km cells randomly sampled from across Britain. The relationship between biodiversity and carbon was significantly different from the national pattern for 34 of 41 of the 100 × 100 km squares, being less negative in all cases (see Table S3). The relationship between biodiversity and agriculture value was also significantly different in 32 of 41, mostly being less positive than the association for Britain as a whole (see Table S4). Finally, for carbon and agriculture value, 28 of

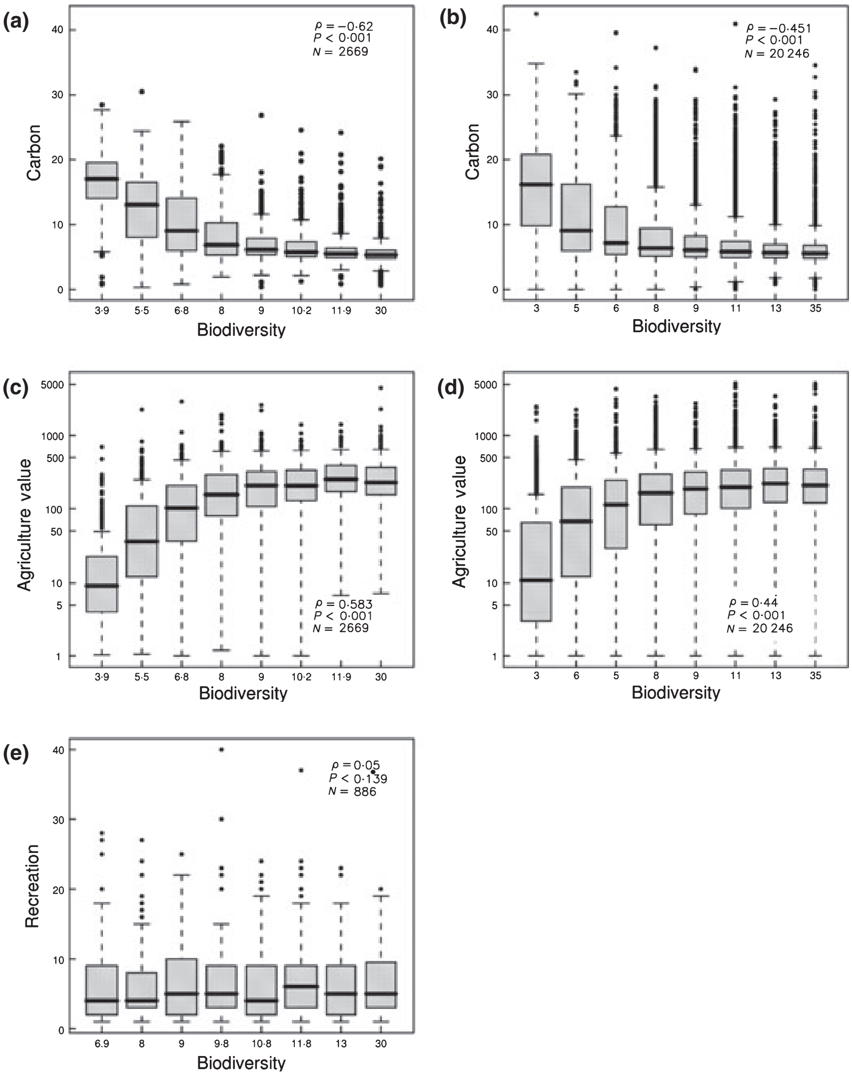

Fig. 2. Associations between Biodiversity and Ecosystem Service Variables. Biodiversity and Carbon at (a) 100 km^2 resolution; and (b) 4 km^2; Biodiversity and Agriculture Value at (c) 100 km^2 resolution; and (d) 4 km^2; and (e) Biodiversity and Recreation at 100 km^2 resolution for England only. For illustrative purposes data on the x-axes were binned by quantiles, for each bin the median (central line), interquartile range (edge of box), range (whiskers) and outliers (dots) of the y-axis values are shown. Spearman rank correlations (ρ, P and n shown on each panel) are based on raw data. Biodiversity here refers to richness of species of conservation concern; for other measures of biodiversity, see Figs S1–S3.

41 of the 100 × 100 km squares showed a significantly different relationship compared with Britain, most being less negative (see Table S5).

REGIONAL VARIATION IN COVARIANCE STRUCTURES

Finally, taking the finest resolution data and the smallest of the spatial extents, we tested the sensitivity of the results to the choice of study area. To this end, we compared the correlations obtained when measured within each 100 × 100 km British National Grid square. This analysis revealed strong regional variation in associations between biodiversity and ecosystem services (Fig. 4; Fig. S4 and Tables S3–S5). Standardizing the sample size by randomly selecting anywhere between 100 and 750 samples reduces the significance of some relationships but not the direction of the associations (for the 100 sample results, see Tables S3–S5). Biodiversity (regardless of the measure used) shows a significant negative relationship with carbon in the wet and cold areas of the north-west and uplands, where low levels of biodiversity are associated with deep peat soils. The opposite is true in the south and east, where high biodiversity is associated with high-carbon habitats, such as forests and wetlands (Fig. 4a). Although slightly less clear, the same regional reversal is seen in the relationship between biodiversity and agriculture value. In this case, biodiversity is significantly positively associated with agriculture value in the north and west, but negatively related in some parts of southern and eastern Britain (Fig. 4b). Carbon vs. agriculture value shows a similar pattern to carbon vs. biodiversity but is slightly less clear with some positive (but non-significant) regions further north (Fig. 4c).

Discussion

In examining the spatial covariance structure between areas important for providing three ecosystem services (carbon storage, agriculture value and recreation) and supporting priority species for conservation, we have found a mixed pattern with some positive relationships, some negative, and sometimes no relationship at all.

At the scale of Britain, habitats that are important carbon stores (generally peat and moorlands) are relatively depauperate in species of conservation concern and there is very little congruence between those cells that are best for carbon and

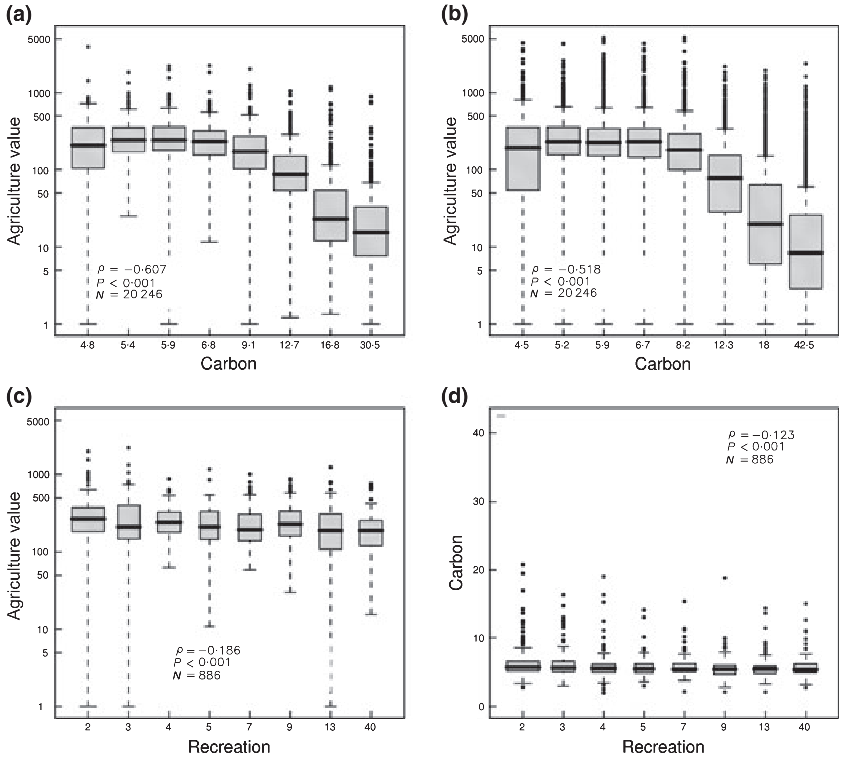

Fig. 3. Associations between Ecosystem Service Variables. Carbon and Agriculture Value for Britain at (a) 100 km^2 resolution and (b) 4 km^2; (c) Recreation and Agriculture Value for England at 100 km^2 resolution; and (d) Recreation and Carbon for England at 100 km^2 resolution. For illustrative purposes data on the *x*-axes were binned by quantiles, for each bin the median (central line), interquartile range (edge of box), range (whiskers) and outliers (dots) of the *y*-axis values are shown. Spearman rank correlations (ρ, *P* and *n* shown on each panel) are based on raw data.

Table 1. Hotspots (overlapping grid squares) for Biodiversity and Ecosystem Services (Carbon, Agriculture Value and Recreation) in Britain. Count is the number of squares (either 100 or 4 km^2) that overlap; per cent total is the per cent of squares that overlap out of the total number of squares in that analysis

		Top 10% overlap		Top 20% overlap		Top 30% overlap	
Resolution	Variables	Count	Per cent total	Count	Per cent total	Count	Per cent total
100 km^2	Biodiversity and carbon	3	0·1	10	0·4	46	1·7
4 km^2	Biodiversity and carbon	39	0·2	218	1·1	737	3·6
100 km^2	Biodiversity and agriculture value	53	2·0	172	6·4	371	13·9
4 km^2	Biodiversity and agriculture value	450	2·2	1521	7·5	2906	14·4
100 km^2	Biodiversity and recreation*	13	1·5	41	4·6	91	10·3
100 km^2	Carbon and agriculture value	3	0·1	14	0·5	32	1·2
4 km^2	Carbon and agriculture value	36	0·2	143	0·7	360	1·8
100 km^2	Recreation* and agriculture value	7	0·8	39	4·4	111	12·5
100 km^2	Recreation* and carbon	8	0·9	32	3·6	74	8·4

*Based on England only.

those that are best for biodiversity, regardless of the measure of biodiversity that we use. As such, the considerable interest in land use policies that encourage more secure carbon storage is unlikely to help to deliver substantially on national-scale biodiversity commitments or to improve the provision of other ecosystem services, such as recreation. In contrast, in their study in the Central Coast region in California, Chan *et al.* (2006) found no relationship between these variables which, while not offering a policy win-win, at least does not suggest the strong trade-off revealed by our study.

The strong positive correlations between habitats that are important for biodiversity and those that provide high-value agriculture might be interpreted as offering greater prospects for policy win-wins. However, this relationship is unlikely to be causative and we suspect that this spatial coincidence is likely to be to the detriment of biodiversity. High-value, intensive, agriculture is largely incompatible with achieving conservation priorities. The high spatial congruence we find suggests that options for spatially separating agriculture and biodiversity though land-sparing strategies (Green *et al.* 2005; Fischer *et al.* 2008) are limited when we consider Britain as a whole. Conservation *within* high agriculture value regions is needed, perhaps through smaller-scale land sparing within these regions (for some species), a broader 'greening' of intensive agriculture (for others) or a combination of both. Chan *et al.* (2006) and Naidoo *et al.* (2008) found only weak (negative and positive respectively) correlations between agriculture and biodiversity, but each only considered the contribution of pasture to livestock production in their estimate of the agricultural value of an ecosystem.

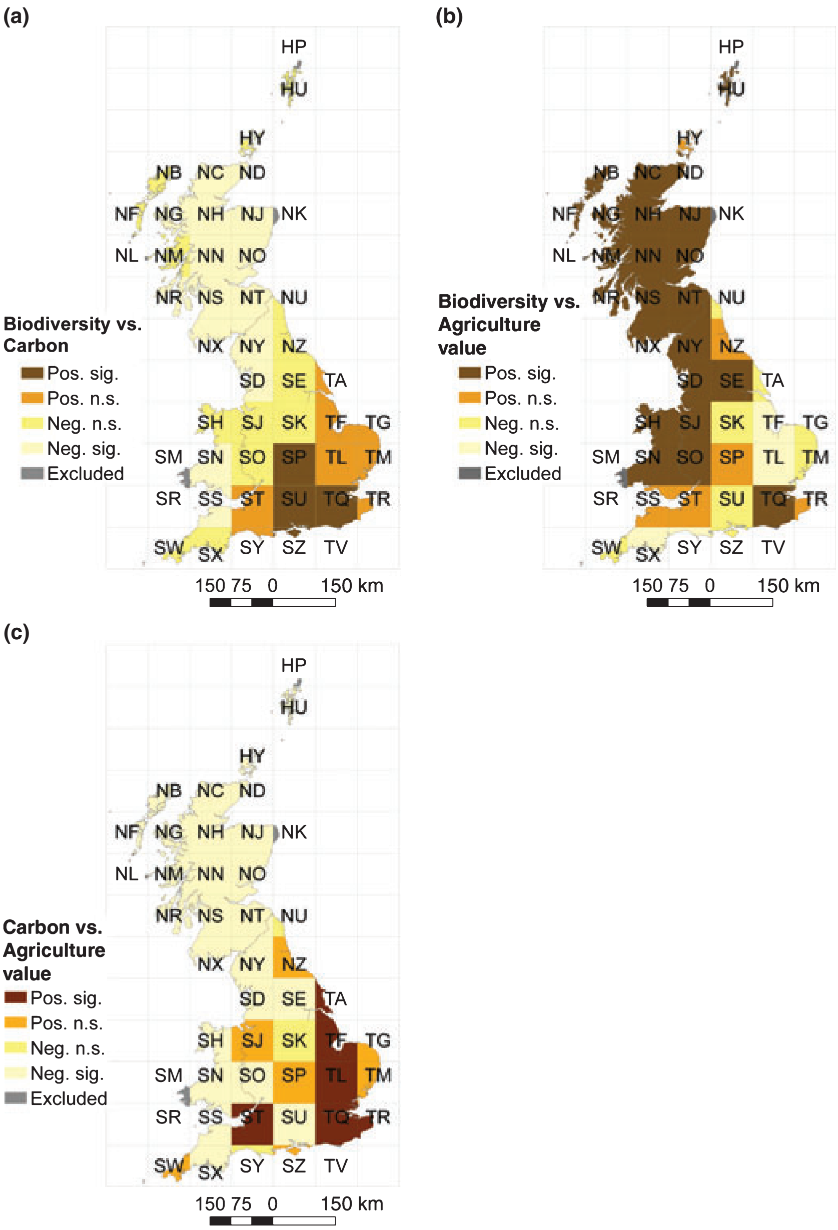

Fig. 4. Regional associations between Biodiversity and Ecosystem Services. (a) Biodiversity and Carbon; (b) Biodiversity and Agriculture Value; and (c) Carbon and Agriculture Value. Regional associations are based on Spearman rank correlations among a subsample (8/25 in every 100 km^2, see text for details) of 4 km^2 squares within each 100 × 100 km British National Grid (BNG) square. Six 100 km × 100 km squares were excluded from the analysis as they contained fewer than 100 4 km^2 squares. See Tables S3–S5 for ρ, *P* and N for each 100 km × 100 km square. See Fig. S4 for alternative measures of biodiversity.

The lack of a relationship between recreation and either of the other ecosystem services or biodiversity suggests that enhancing recreation requires bespoke policy approaches designed for the landscapes where people live, work and play at highest densities (Ruliffson *et al.* 2003; Önal & Yanprechaset 2007), something that is poorly provided by current conservation and land use strategies in Britain (Eigenbrod *et al.* 2009).

When we tested the sensitivity of these national-scale covariance structures to the spatial resolution of the data, we found that correlations were weaker at finer resolutions but the spatial overlap of priority grid squares increased. This agrees with the findings of some studies of patterns of biodiversity priorities, which show declines in correlations between the richness of different higher taxa at finer spatial resolutions (Pearson & Carroll 1999; Grenyer *et al.* 2006). In our analyses, varying the spatial resolution of the data did not, however, change the underlying covariance structures. One might ask what the 'ideal' resolution of the data to perform such analyses would be. The answer probably depends on what resolution the data permit (for example, insufficient sampling points preclude us from analysing the recreation data at the finer resolution) and over what resolution the ecosystem services provided by different habitats show significant variation. But perhaps the most meaningful resolution for analyses is set by that over which decisions regarding the management of habitats are taken. The very small size of agricultural land parcels and habitat patches more generally in Britain suggests that our analyses at the finer resolution may be reasonable for many questions in this region. Of course management agreements need to reflect the spatial scale of the biological processes that are important (e.g. species home ranges size, blanket bog formation) as well as land parcel size.

When varying the spatial extent of analyses, we found that relationships between biodiversity and ecosystem services tended systematically to shift in form. Our results thus provide an interesting supply-side counterpart to the demand-side study of Kremen *et al.* (2000), who examined beneficiaries of ecosystem services in Madagascar. These authors showed that whether habitat conservation could be justified on economic grounds depended on the scale over which benefits were measured. At local and global scales, conservation benefits outweighed those offered by development, but the balance swung the other way when only considering national-scale benefit flows. Again, we would argue that the most relevant scale for most analyses is set by the legislative or policy context being analysed.

The most challenging set of results from our sensitivity testing are those presented by the regionalization analysis, which shows that one can arrive at diametrically opposing conclusions about relationships between ecosystem services and biodiversity by studying the same question within different areas, even within a relatively small island. Moreover, the trends were remarkably robust to the different measures of biodiversity used (Figs S1–S3). In a policy context, the location-specific nature of these relationships underscores the importance of multi-service, regional-scale policies for the delivery of ecosystem services and biodiversity management. Interestingly, writings on conservation planning for biodiversity have tended instead to favour vertical integration of governance to national scales (Erasmus *et al.* 1999; Strange *et al.* 2006). The push towards vertical integration has been driven by the nature of spatial turnover in biodiversity, a process that may not be reflected in ecosystem services such as carbon storage. Our results also pose a scientific challenge to those hoping to derive generalities about the nature of biodiversity and ecosystem service relationships. As in some other areas of ecology (Roughgarden, Pennington & Alexander 1994), our results suggest that efforts to establish general patterns of congruence in ecosystem services and biodiversity may offer a less constructive way forward than a more spatially explicit approach.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1. Associations between *Bird* Biodiversity and Ecosystem Service Variables.

Figure S2. Associations between *Butterfly* Biodiversity and Ecosystem Service Variables.

Figure S3. Associations between *Bird/Butterfly/BAP* Biodiversity and Ecosystem Service Variables.

Figure S4. Regional associations for alternative measures of Biodiversity and Ecosystem Services.

Table S1. Summary of values used in calculating the gross margin of agriculture value

Table S2. Hotspots (overlapping grid squares) for alternative measures of Biodiversity and Ecosystem Services (Carbon, Agriculture Value & Recreation)

Table S3. Regional associations between Biodiversity and Carbon

Table S4. Regional associations between Biodiversity and Agriculture value

Table S5. Regional associations between Carbon and Agriculture value

Appendix S1. Calculation of production values for agriculture

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