

Ecosystem service benefits of contrasting conservation strategies in a human-dominated region

Felix Eigenbrod, Barbara J. Anderson, Paul R. Armsworth, Andreas Heinemeyer, Sarah F. Jackson, Mark Parnell, Chris D. Thomas and Kevin J. Gaston

Proc. R. Soc. B 2009 **276**, doi: 10.1098/rspb.2009.0528 first published online 27 May 2009

Supplementary data

["Data Supplement"](#)

<http://rspsb.royalsocietypublishing.org/content/suppl/2009/05/25/rspb.2009.0528.DC1.html>

References

[This article cites 40 articles, 13 of which can be accessed free](#)

<http://rspsb.royalsocietypublishing.org/content/276/1669/2903.full.html#ref-list-1>

[Article cited in:](#)

<http://rspsb.royalsocietypublishing.org/content/276/1669/2903.full.html#related-urls>

Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (1299 articles)

[environmental science](#) (196 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Ecosystem service benefits of contrasting conservation strategies in a human-dominated region

Felix Eigenbrod¹, Barbara J. Anderson², Paul R. Armsworth¹,
Andreas Heinemeyer³, Sarah F. Jackson^{1,†}, Mark Parnell^{1,‡},
Chris D. Thomas² and Kevin J. Gaston^{1,*}

¹*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

²*Department of Biology, University of York, PO Box 373, York YO10 5YW, UK*

³*Stockholm Environment Institute York-Centre, Department of Biology, University of York, Grimston House, York YO10 5DD, UK*

The hope among policy-makers and scientists alike is that conservation strategies designed to protect biodiversity also provide direct benefits to people by protecting other vital ecosystem services. The few studies that have examined the delivery of ecosystem services by existing conservation efforts have concentrated on large, ‘wilderness’-style biodiversity reserves. However, such reserves are not realistic options for densely populated regions. Here, we provide the first analyses that compare representation of biodiversity and three other ecosystem services across several contrasting conservation strategies in a human-dominated landscape (England). We show that small protected areas and protected landscapes (restrictive zoning) deliver high carbon storage and biodiversity, while existing incentive payment (agri-environment) schemes target areas that offer little advantage over other parts of England in terms of biodiversity, carbon storage and agricultural production. A fourth ecosystem service—recreation—is under-represented by all three strategies. Our findings are encouraging as they illustrate that restrictive zoning can play a major role in protecting natural capital assets in densely populated regions. However, trade-offs exist even among the four ecosystem services we considered, suggesting that a portfolio of conservation and sustainability investments will be needed to deliver both biodiversity and the other ecosystem services demanded by society.

Keywords: biodiversity; ecosystem services; protected areas; sustainability; land management

1. INTRODUCTION

Both biodiversity and other ecosystem services—the benefits that humans derive from ecosystems—are increasingly threatened by human activities (Millennium Ecosystem Assessment 2005). The hope among conservation biologists and policy-makers alike is that existing and future conservation strategies can deliver not only biodiversity, but also other ecosystem services (Janzen 1998; Balvanera *et al.* 2001; Millennium Ecosystem Assessment 2005; Daily & Matson 2008; Goldman *et al.* 2008). However, there is limited evidence that biodiversity priorities covary with other ecosystem services (Chan *et al.* 2006; Naidoo *et al.* 2008), and only a few case studies have shown that areas set aside to conserve biodiversity also provide additional ecosystem services (e.g. Ricketts *et al.* 2004; Russ *et al.* 2004). A more comprehensive understanding of how effective existing biodiversity conservation

strategies are in providing both biodiversity and other ecosystem services thus remains one of the ecological issues currently most relevant to policy-makers (Odling-Smee 2005; Sutherland *et al.* 2006).

Particularly little is known about the performance of conservation strategies other than large, North American-style ‘wilderness’ areas (IUCN category I and II protected areas; IUCN 1994) in delivering ecosystem services other than biodiversity. While such areas are ideal for protecting ecosystem services with global benefits such as carbon sequestration, the primary benefits for many services only apply at much smaller spatial scales (Hein *et al.* 2006). This is problematic as most of the world’s population does not live in or near large wilderness reserves (e.g. Scott *et al.* 2001; Loucks *et al.* 2008), and consequently will receive only some benefits from many of the ecosystem services delivered by such areas. Indeed, an increasing number of regions are so densely populated that they entirely lack extensive wilderness areas, including parts of the eastern seaboard of the USA, southeast Asia, western Europe, the Atlantic forests of Brazil and large parts of India (Kareiva *et al.* 2007). The need to protect ecosystem services within human-dominated landscapes has been recognized by practitioners; a recent survey showed that conservation

* Author for correspondence (k.j.gaston@sheffield.ac.uk).

† Present address: Penny Anderson Associates Ltd, Park Lea, 60 Park Road, Buxton, Derbyshire SK17 6SN, UK.

‡ Present address: En:mapping, 38, Talbot Street, Sheffield S2 2TG, UK.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0528> or via <http://rsb.royalsocietypublishing.org>.

projects that focus on ecosystem service provision in addition to biodiversity protection are more likely to be found in agricultural landscapes than those that focus on biodiversity conservation alone (Goldman *et al.* 2008). Several studies have now examined the distribution and covariance of biodiversity and other ecosystem services in human-dominated landscapes (Chan *et al.* 2006; Egoh *et al.* 2009), with Chan *et al.* also comparing the performance of multiple *hypothetical* conservation networks in delivering multiple ecosystem services in California. However, no spatial analyses of ecosystem service delivery by *existing* conservation strategies within such human-dominated landscapes exist.

Two major strategies to conserve biodiversity within human-dominated landscapes are restrictive zoning and incentive payments to private landowners. The former involves using planning legislation to restrict human development (Beatley 2000), while the latter provides payments to rural landholders in return for management actions designed to increase biodiversity (e.g. agri-environment or set-aside schemes). Investments in these strategies are substantial; for example, the European Union spends approximately €3.7 billion yr⁻¹ on various agri-environment schemes (Kleijn *et al.* 2006), and the USA spent \$1.8 billion in 2007 on the equivalent Conservation Reserve Program (United States Department of Agriculture 2008). However, analyses of whether these types of conservation strategy deliver ecosystem services other than biodiversity remain wanting, despite increasing awareness that effective management of ecosystem services must incorporate a wide range of policy instruments including incentive-based approaches (Daily & Matson 2008; Jack *et al.* 2008).

Here, we compare the delivery of biodiversity and three other ecosystem services (carbon storage, agricultural production and rural recreation) by three conservation strategies (protected areas, restrictive zoning and incentive payments to landowners) in England. England has a high population density, with 393 people km⁻² (National Statistics 2005); the average population density worldwide is 45 people km⁻² (Central Intelligence Agency 2008). England also has no wilderness regions (*sensu* Sanderson *et al.* 2002). It is thus a good example of the type of 'domesticated nature' (Kareiva *et al.* 2007) that will increasingly describe locations where much of the world's population lives. In addition, England represents a good test of the effectiveness of different types of conservation strategies in delivering ecosystem services because protected areas, restrictive zoning and incentive payment schemes are all well developed, covering over 35 per cent of the total terrestrial area (130 439 km²) (figure 1). Finally, relatively high quality and resolution data on biodiversity and ecosystem services are available for England (figure 2).

2. MATERIAL AND METHODS

Our overall approach to assess the performance of conservation strategies in delivering ecosystem services was to calculate whether the amount of a given ecosystem service that was present in a given strategy was more or less than would be expected for the area of the strategy.

(a) Conservation strategies

We considered all areas with statutory protection designated primarily for biodiversity conservation to be Protected Areas.

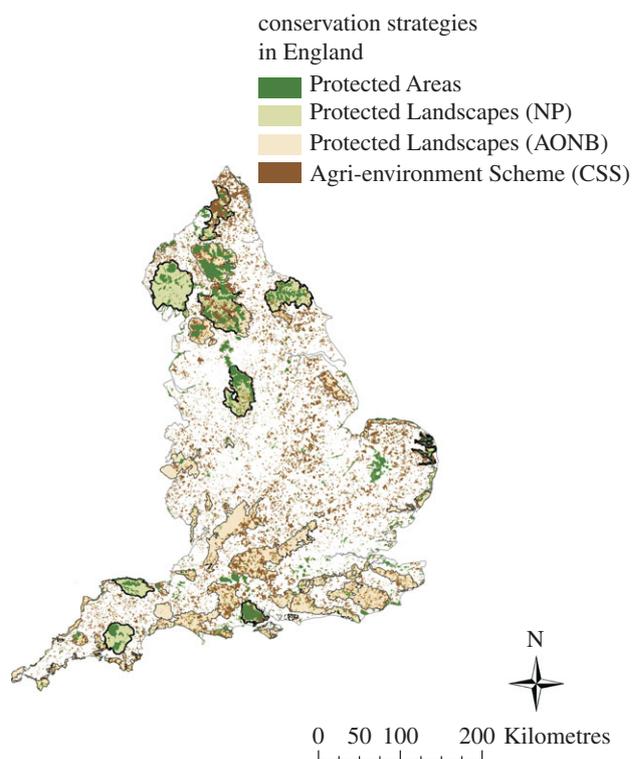


Figure 1. Distribution of conservation strategies in England. AONB, 'Area of Outstanding Natural Beauty'; NP, 'National Park'; CSS, 'Countryside Stewardship Scheme'.

These included Local Nature Reserves, National Nature Reserves, Special Areas of Conservation, Special Protection Areas, Sites of Special Scientific Interest and Ramsar sites (Jackson & Gaston 2008a); we only include those that fall within the land area of England here, excluding estuaries and offshore islands. These Protected Areas form the backbone of biodiversity conservation in England, and cover 6.3 per cent of the land area. They are generally small (93% cover 100 ha or less), and over half are on private land (Jackson & Gaston 2008a). None of these Protected Areas exclude human uses altogether; indeed many are heavily managed through specific agricultural or forestry practices to conserve a particular habitat of conservation concern (Marren 1994). England also contains two types of Protected Landscapes—National Parks and Areas of Outstanding Natural Beauty—which cover 8.0 and 15.3 per cent of the country, respectively (excluding the offshore Isles of Scilly). These Protected Landscapes are primarily managed through restrictive zoning, with the goal of conserving 'natural beauty' and providing outdoor recreation while still supporting rural industries (Natural England 2008). England, like much of western Europe, also has an extensive programme of incentive payments to landowners to promote wildlife-friendly farming (Agri-environment Schemes). The largest of these schemes—the Countryside Stewardship Scheme (CSS)—covers 15.9 per cent of England. The area covered by Agri-environment Schemes in England changes from year to year; we used the most current data available. For the CSS agreements this was 11 June 2007.

The GIS boundary layers for Protected Landscapes and Agri-environment Schemes were obtained from www.magic.gov.uk in July 2008, while those for the Protected Areas were obtained from various sources (see Jackson & Gaston 2008a for details). Spatial overlaps of these three strategies are typically quite low, and while a substantial proportion

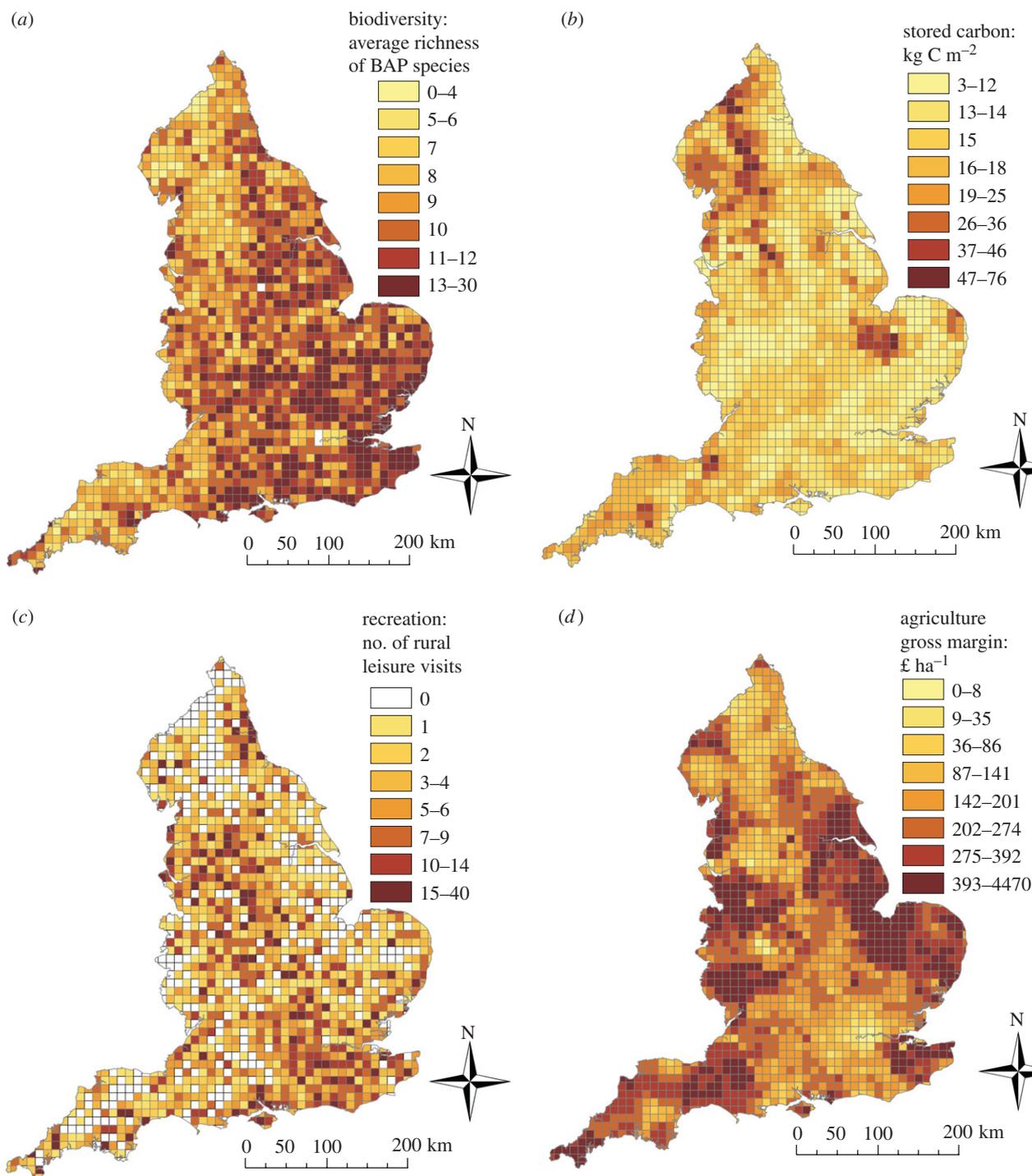


Figure 2. (a) Distribution of biodiversity, (b) carbon storage, (c) recreation and (d) agricultural production in England at the 10 km grid square resolution. The 10 km resolution is used for display purposes only; finer resolution data were used for the analyses (§2).

of land covered by Protected Areas lies also within Protected Landscapes, the converse is not true (table 1).

(b) Ecosystem services

Mapping the distribution of most ecosystem services is difficult due to a lack of data (Naidoo *et al.* 2008). Consequently, the majority of existing studies mapping the distribution of ecosystem services either estimate ecosystem services from proxies (e.g. Chan *et al.* 2006 for recreation; Turner *et al.* 2007 for all services globally), or use coarse-resolution datasets (e.g. Naidoo & Iwamura 2007 for agricultural

production; Egho *et al.* 2008 for carbon storage). However, such data are unsuitable for assessing the performance of conservation strategies in England, given the fine scale and degree of fragmentation of Protected Areas and Agri-environment Schemes (figure 1). We thus limited our analyses to the four ecosystem services for which we were able to obtain high-resolution data for the whole of England: biodiversity (UK Biodiversity Action Plan (BAP) species), carbon storage (total soil + vegetation), agricultural production (gross margin) and recreation (representative sample of day visits to rural locations for the English population as a whole).

Table 1. Extent of overlap of conservation strategies in England.

strategy	overlaps with	proportion overlap
Protected Areas	Protected Landscapes	0.63
	Agri-environment Scheme	0.25
Protected Landscapes	Protected Areas	0.17
	Agri-environment Scheme	0.23
Agri-environment Scheme	Protected Areas	0.10
	Protected Landscapes	0.34

(i) Biodiversity

We used the recorded presences of 326 terrestrial BAP (Anon. 1994) (<http://www.ukbap.org.uk/>, accessed April 2008) species (bryophytes, vascular plants, butterflies, herptiles, birds and mammals) present in England as our measure of biodiversity. We obtained the recorded presences of all BAP bryophytes, vascular plants, butterflies, herptiles and mammals present in England, using data at the 2×2 km grid resolution held at the Centre for Ecology and Hydrology Biological Records Centre. For birds, we used the British Trust for Ornithology timed visits to tetrads (2×2 km grid resolution) from the 1988–1991 Breeding Bird Atlas (Gibbons *et al.* 1993) to produce modelled probabilities of occurrence for all tetrads within England (Franco *et al.* 2009). These probabilities were converted to binary presence/absence data so that a ‘Presence’ of a bird species in any square was designated where the likelihood of occurrence was higher than a species-specific cut-off (supplementary methods and table S1 in the electronic supplementary material). We used BAP species as our measure of biodiversity as these ‘species of conservation concern’ arguably require the greatest protection in order to persist.

(ii) Carbon storage

The carbon storage layer is an estimate of combined organic soil and above ground vegetation carbon (in kg C) calculated at the 1×1 km grid resolution. We obtained vegetation carbon data at the 1 km grid resolution from the Centre for Ecology and Hydrology (Milne & Brown 1997). 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 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 per cent 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 soil carbon content (e.g. towns, roads 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. This may lead to a slight overestimation of soil carbon within built-up areas and roads. However, as urban areas already have the lowest carbon levels in England in this layer, this potential bias will have very little effect on the results.

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 spatially delineated using GIS to include only the land area of England as described earlier.

(iii) 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 one day in duration made from home (or a holiday destination in England) for leisure purposes (Natural England 2006).

We also quantified the relationship between recreational use of the countryside and human population density, as the latter has been shown to be a main driver of the former (Hörnsten & Fredman 2000). We used a two-tailed *t*-test to compare the average population density in the vicinity (17.3 km radius) of visits to Protected Areas, Protected Landscapes and areas included in the CSS with the average population density in the vicinity of visits to the wider countryside. We calculated population density within 17.3 km of the point locations of these visits as this corresponded to the average distance travelled for visits to the countryside (Natural England 2006). We calculated population density by first downloading 2001 national census boundaries at the highest spatial resolution available (output area) from UKBorders and the total resident population of these output areas from CasWeb. We then used these datasets to create a population density surface at the 2×2 km grid resolution using the freely available software package SURFACEBUILDER (Martin 2007).

(iv) Agriculture

The agricultural production layer is the summed gross margin of all major crops and livestock. 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). Agricultural census data (Department for Environment, Food and Rural Affairs 2005) collected at ward/local authority resolution (mean area 1912 ha) were converted into gross margins based on information from the Farm Management Handbook 2007/2008 (Beaton *et al.* 2007) (supplementary methods and table S2 in the electronic supplementary materials).

(c) Elevation

Protected Areas are known to be biased towards uplands in Britain (Jackson & Gaston 2008a). To quantify this

Table 2. Provision of biodiversity and ecosystem services under three conservation strategies. AONB, 'Area of Outstanding Natural Beauty'; NP, 'National Park'; CSS, 'Countryside Stewardship Scheme'. A ratio of >1 indicates that an ecosystem service is over-represented; values <1 indicate under-representation. The percentage of the total amount of biodiversity (summed proportion of ranges) and other ecosystem services in England is given for each conservation strategy. 'All conservation strategies' refers to the area covered by either Protected Areas, Protected Landscapes or the CSS Agri-environment Scheme.

	Protected Areas		Protected Landscapes				Agri-environment Schemes		all conservation strategies	
			NP		AONB		CSS			
	% of total	ratio	% of total	ratio	% of total	ratio	% of total	ratio	% of total	ratio
biodiversity	18.8	3.33	14.1	1.71	28.4	1.78	13.7	0.99	55.8	1.59
carbon storage	11.4	1.80	12.9	1.61	16.3	1.06	17.1	1.08	42.1	1.17
recreation	5.6	0.88	6.0	0.75	13.5	0.88	10.4	0.66	27.9	0.78
agriculture	2.5	0.40	3.7	0.46	12.9	0.84	16.0	1.01	29.9	0.83

relationship for all conservation strategies, we calculated the mean elevation for Protected Areas, Protected Landscape, Agri-environment Schemes and for England as a whole, using the GTOPO30 digital elevation model (<http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html>).

(d) Calculation of representation of ecosystem services

We divided the percentage of each of the measures of ecosystem services contained within a conservation strategy by the percentage land area covered by that strategy to quantify the extent to which ecosystem services are represented by the different conservation strategies. A value greater than one thus indicates that a particular strategy contains a disproportionately large amount of a specific ecosystem service relative to the area that it covers (table 2). For the ecosystem service layers other than biodiversity, we spatially delineated each layer by the exact extent of a conservation strategy. However, we were only able to delineate representation of biodiversity within conservation strategies at the 2 × 2 km grid resolution. This was because our measure of biodiversity was the summed proportion of the ranges of all BAP species, and each species was either 'present' or 'absent' in a 2 × 2 km grid cell. A strategy was considered as present in a grid cell (for biodiversity) if at least 40 per cent of the cell was covered by that strategy. This threshold resulted in the best match between the actual percentage of England covered by conservation strategies and the percentage estimated based on presence/absence at the 2 × 2 km grid resolution; conclusions are not sensitive to the threshold selected (table S3 in the electronic supplementary material). All GIS analyses were carried out in ARCGIS/ARC/INFO 9.2 (ESRI, Redlands, CA, USA).

(e) Calculation of distribution of land cover types within conservation strategies

The distribution of ecosystem services in an area will largely depend on the locations and amount of the land cover types within the area. To assess this, we calculated for each conservation strategy and also for the wider countryside (i.e. places not covered by any conservation strategy) the percentage areas covered by deciduous forest, coniferous forest, pasture/grassland, crop land, heather moorland, wetland and urbanization/roads. We used the Land Cover Map 2000 (25 × 25 m resolution) (Fuller *et al.* 2002) as the basis

for this analysis (tables S4 and S5 in the electronic supplementary material).

3. RESULTS AND DISCUSSION

Protected Areas are well placed to protect species of conservation concern, capturing 3.3 times as much biodiversity as would be expected for their area (table 2). This relationship holds across all species groups considered (table S6 in the electronic supplementary material). The species in the smallest quartile of range sizes are more than twice as well represented as those in the largest range size quartile (4.3 versus 1.9 times the level of representation one would have expected based on area alone). Carbon storage is also well represented (1.8 times expected representation), reflecting the over-representation of the carbon-rich soils in heather moorland and wetland in Protected Areas (23 and 9% of Protected Areas land versus 3 and 1% of England as a whole, respectively; table S5 in the electronic supplementary material). Low coverage of cropland (6% of Protected Areas land, compared with 36% of England as a whole; table S5 in the electronic supplementary material) means that agricultural production is under-represented in Protected Areas (0.40); this is also the case for recreation (0.88) (table 2). Thus, Protected Areas contribute substantially to their primary goal of biodiversity conservation, and coincidentally to carbon storage. But these areas provide little protection for the other two ecosystem services considered here.

Protected Landscapes are intended as multi-use landscapes (Natural England 2008), and partially achieve this (table 2). Representation of biodiversity is nearly twice what is expected given the area, but still only half as high as in Protected Areas. Carbon storage is nearly as well represented in National Parks (1.61 times expected representation) as in Protected Areas (1.80 times expected representation), but Areas of Outstanding Natural Beauty are merely average in their representation of carbon storage. In addition, 41 of the 70 species not present within Protected Areas (which contain 256 of the BAP species) occur in Protected Landscapes, indicating that Protected Landscapes complement Protected Areas. Protected Landscapes and other forms of restrictive zoning may thus play an important role in providing the type of

supplementary protection for biodiversity outside Protected Areas that is required if biodiversity is to be maintained within human-dominated landscapes (Maiorano *et al.* 2008). Protected Landscapes are more reflective of England in terms of overall land cover than Protected Areas, but still have a considerably lower proportion of their area covered by cropland and urbanization and a higher proportion of area covered by heather moorland, wetland and forests than England as a whole (table S5 in the electronic supplementary material). This is reflected in the under-representation of agricultural production within Protected Landscapes, though this is much less pronounced than within Protected Areas. Recreation is again under-represented (table 2), despite the fact that public appreciation of these landscapes was a major motivation in their designation (Natural England 2008).

Incentive payments to farmers under the CSS are scattered relatively evenly across farmland throughout England (figure 1). At first glance, these areas appear to be a representative selection of England as a whole in terms of biodiversity, carbon storage and agricultural production, all three of which have values close to one (table 2). However, areas within the CSS actually have a higher proportion of their area covered by crops (45%) than England (36%), and much less roads and urban development (3% of the area versus 10% of England); all other land cover types are present in similar proportions to England (table S5 in the electronic supplementary material). This suggests that cropland within the CSS is less productive per unit area. It is difficult to say if this is due to wildlife-friendly farming practices *per se* or simply because farmers generally enrol less productive areas into the CSS. In addition, recreational benefits are even more under-represented within areas in the CSS than within Protected Areas or Protected Landscapes (table 2). A new incentive payment scheme, the HLS, was introduced in 2005 (Smallshire *et al.* 2004). While not yet fully deployed, this new scheme may prove more effective than the CSS in representing biodiversity. The first locations included in the HLS contain 1.70 times the level of biodiversity expected for their area (table S7 in the electronic supplementary material). This provides the first evidence that this new incentive payment strategy may be fulfilling its policy objectives (provided that the first-established locations are representative of those that will follow), albeit at a cost in agricultural production (0.89 times expected representation).

The extent to which the relationships documented are causal is important to future decisions about land management designations. Representation of carbon and agricultural production was not driven by the management type *per se*, but rather by land cover type—as discussed earlier—and by altitude. The two strategies that are disproportionately distributed in the uplands (mean elevation of Protected Areas is 222 m; National Parks is 266 m; England overall is 106 m) represent carbon storage well, but agriculture poorly; Protected Areas are biased towards upland areas in much of the world (Loucks *et al.* 2008). By contrast, the CSS Agri-environment Scheme and the AONB system of Protected Landscapes, which have greater coverage in the lowlands (average elevation 121 and 150 m, respectively), provide approximately average representation of both carbon storage and agriculture. Recreation was under-represented

by all conservation strategies, probably because a main driver of use of the countryside for recreation is human population density. Population density is twice as high in the vicinity (within 17.3 km) of visits to the wider countryside as it is in the vicinity of visits to areas currently enjoying protection under the three different conservation strategies (609 ± 9.10 s.d. inhabitants km^{-2} outside and 305 ± 9.11 s.d. inhabitants km^{-2} within conservation areas $t = 19.4$, $n = 6279$, $P \sim 0$). Finally, it is difficult to say whether the high representation of biodiversity achieved by the Protected Areas and Protected Landscapes is causal. These areas might have high representation even without designation, simply due to their being in areas of England that are poorly suited to intensive agricultural production (see Gaston *et al.* 2008 for a review of this issue). It is, however, clear from earlier work (Jackson & Gaston 2008b) that over half of the BAP (species of conservation concern) species are mostly or entirely present within Protected Areas, with our results showing that Protected Landscapes provide protection for a further subset of these species.

While the level of detail presented here represents an improvement on previous large-scale work on ecosystem services (Costanza *et al.* 1997; Chan *et al.* 2006; Turner *et al.* 2007; Egoh *et al.* 2008; Naidoo *et al.* 2008), our study is still constrained by the limited availability of data on ecosystem services; this remains a major obstacle to the understanding and protection of these vital resources (Naidoo *et al.* 2008). In particular, the mismatch between the ward-level resolution of the agricultural production layer (mean area 1912 ha) and average size of Agri-environment Scheme parcels (mean area 134 ha) or Protected Areas (93% less than 1 ha in size) may have led to overestimates of agricultural production in these areas. This is because the estimate of agricultural production for parcels was based on the average production within each ward; if most of a ward was not within a conservation strategy but intensively farmed, then estimates for any conservation strategy within the ward would have been too high. This may also have been an issue for carbon storage (100 ha resolution), though here an underestimate of carbon storage in very small parcels of woodland within agricultural land is more likely to have occurred than any overestimation. Such bias is likely to have had little effect on the overall pattern of the distribution of carbon storage, though, as most English carbon is found in soils and not vegetation (Milne & Brown 1997). In addition, we quantify only the current representation of ecosystem services by existing conservation strategies, not their long-term protection. Time-series data would be needed to determine their effectiveness in ensuring long-term protection of ecosystem services, but are unavailable at the scale of this analysis; acquiring such data should clearly also be a future research objective in the evaluation of ecosystem service provision. Finally, ecosystem services other than the four we consider here may have very different distributions and hence representation by English conservation strategies. For example, the areas most important for carbon sequestration may not be the peat of the uplands, where most carbon is stored in England, as soil carbon may be declining in England and Wales (Bellamy *et al.* 2005). The distribution of pollination services, on the other hand, could be linked to the juxtaposition of semi-natural habitats with

large amounts of animal-pollinated crops (Ricketts *et al.* 2008) (e.g. the apple orchards of Kent in the southeast of England).

Notwithstanding the above caveats, these findings have wide-ranging policy implications because they provide the first illustration of how well conservation strategies in human-dominated landscapes represent biodiversity and three other key ecosystem services. Our results indicate that achieving both high agricultural production and biodiversity is difficult within a single land management system, indicating that some 'land sparing' (Green *et al.* 2005) is necessary to achieve biodiversity targets. We show that protected areas and restrictive zoning within a human-dominated landscape are, like large wilderness areas, effective in achieving carbon storage goals (see Xue & Tisdell 2001 and Naidoo & Ricketts 2006 for examples of the latter). However, recent modelling work on biodiversity and carbon sequestration trade-offs (Nelson *et al.* 2008) in the human-dominated Willamette Basin of Oregon suggests that the 'win-win' biodiversity/carbon storage scenario we observed will not always be possible. Clearly, more work is needed to establish under what circumstances (if any) general patterns exist in the correlations between ecosystem services and conservation investments.

Our finding that recreation was under-represented by all conservation strategies contradicts earlier work that suggested that future conservation strategies optimized for biodiversity will also provide good coverage of recreation (Chan *et al.* 2006). This discrepancy is perhaps due to differences in methods—recreation was previously estimated from proxies (Chan *et al.* 2006) while we had representative sampling of rural recreation for the population of England as a whole. We show that conservation investments near urban areas are most valuable for providing opportunities for rural recreation, a result that is probably true worldwide (Hörnsten & Fredman 2000). Representation of recreation is high in Protected Landscapes near large urban centres (e.g. the New Forest and Peak District National Parks have 1.8 and 1.3 times expected representation, respectively), suggesting that recreation visitors would probably visit such areas more often were they closer to home.

Our findings also raise some interesting avenues for future work. For one, optimization of conservation strategies for multiple ecosystem services (e.g. Chan *et al.* 2006) is possible. We did not include such analyses here as our goal was to assess the performance of *existing* conservation strategies in maintaining ecosystem services. The policy relevance of optimizations may be limited in the English context in any case, as the relevant authority for conservation (Natural England) currently has no mandate to conserve ecosystem services. Natural England thus cannot legally disinvest in any of the existing conservation infrastructure and shift resources to areas with high levels of multiple ecosystem services (Nature Conservancy Council 1989; Stroud *et al.* 2001; McLeod *et al.* 2005). Incorporating landscape connectivity measures into the assessment of the representation of biodiversity (e.g. Moilanen *et al.* 2005) and human responses to changes in conservation policy (e.g. Armsworth *et al.* 2006) would also be very interesting, but is beyond the scope of this study. Finally, finer-scale, more mechanistic analyses of which land cover types provide the four ecosystem services considered here would be

very useful. Again, this is beyond the scope of this study, partially as such data are still largely lacking, but mainly as our goal here was to examine the national-scale performance of these three conservation strategies for England, as such assessments are particularly relevant to shaping government policy (e.g. National Audit Office 2008).

In summary, our findings raise three key points with global implications. (i) Past investments in conservation within human-dominated landscapes can, like those made in wilderness areas, provide both key ecosystem service and biodiversity benefits. (ii) Relying on a portfolio of contrasting conservation strategies offers greater protection to biodiversity and other ecosystem services than relying on any one approach. But ultimately, (iii) there are limits to the multifunctionality of landscapes with some trade-offs (biodiversity and agricultural productivity) being inevitable, and some services (recreation) currently falling through the policy cracks.

This work was conducted during a U.K. Population Biology Network (UKPopNet) project ('Linking biodiversity and ecosystem services: processes, priorities and prospects'), which was funded by the Natural Environment Research Council and Natural England. K.J.G. was supported by the Royal Society and the Leverhulme Trust. Many thanks to A. Darlow, S. Gillings, M. Hill, G. Hinton, J. Hopkins, P. Ineson, D. Martin, D. Roy and C. Swanwick for valuable discussions and comments, to three anonymous reviewers whose comments greatly improved the manuscript and to the British Trust for Ornithology, Centre for Ecology and Hydrology, Natural England, and the Department for Environment, Food and Rural Affairs (DEFRA) for providing data. Soil data were supplied by the National Soil Research Institute under a DEFRA funded project 'UK soil database for modelling soil carbon fluxes and land use for the national carbon dioxide inventory'. This work is based on data provided through EDINA UKBORDERS with the support of the ESRC and JISC and uses boundary material that is copyright of the Crown.

REFERENCES

- Anon. 1994 *Biodiversity: the UK Action Plan*. London, UK: HMSO. Cm, 2428.
- Armsworth, P. R., Daily, G. C., Kareiva, P. & Sanchirico, J. N. 2006 Land market feedbacks can undermine biodiversity conservation. *Proc. Natl Acad. Sci. USA* **103**, 5403–5408. (doi:10.1073/pnas.0505278103)
- Balvanera, P. *et al.* 2001 Conserving biodiversity and ecosystem services. *Science* **291**, 2047. (doi:10.1126/science.291.5511.2047)
- Beatley, T. 2000 Preserving biodiversity. *J. Am. Plann. Assoc.* **66**, 5–20. (doi:10.1080/01944360008976080)
- Beaton, C., Catto, J. & Kerr, G. (eds) 2007 *The farm management handbook 2007/2008*. Edinburgh, UK: Scottish Agricultural College.
- Bellamy, P. H., Loveland, P. J., Bradley, R. I., Lark, R. M. & Kirk, G. J. D. 2005 Carbon losses from all soils across England and Wales 1978–2003. *Nature* **437**, 245–247. (doi:10.1038/nature04038)
- Central Intelligence Agency 2008 *The world factbook*. See <https://www.cia.gov/library/publications/the-world-factbook/geos/xx.html>.
- Chan, K. M. A., Shaw, M. R., Cameron, D. R., Underwood, E. C. & Daily, G. C. 2006 Conservation planning for ecosystem services. *Plos Biol.* **4**, e379. (doi:10.1371/journal.pbio.0040379)

- Costanza, R. *et al.* 1997 The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260. (doi:10.1038/387253a0)
- Daily, G. C. & Matson, P. A. 2008 Ecosystem services: from theory to implementation. *Proc. Natl Acad. Sci. USA* **105**, 9455–9456. (doi:10.1073/pnas.0804960105)
- Department for Environment, Food and Rural Affairs 2005 *June Agricultural Survey 2004*. See http://www.defra.gov.uk/esg/work_html/publications/cs/farmstats_web/2_SURVEY_DATA_SEARCH/COMPLETE_DATASETS/NUTS/nuts_excel_2004.zip.
- Egoh, B. *et al.* 2008 Mapping ecosystem services for planning and management. *Agric. Ecosyst. Environ.* **127**, 135–140. (doi:10.1016/j.agee.2008.03.013)
- Egoh, B., Reyers, B., Rouget, M., Bode, M. & Richardson, D. M. 2009 Spatial congruence between biodiversity and ecosystem services in South Africa. *Biol. Conserv.* **142**, 553–562. (doi:10.1016/j.biocon.2008.11.009)
- Franco, A. M. A. *et al.* 2009 Surrogacy and persistence in reserve selection: landscape prioritization for multiple taxa in Britain. *J. Appl. Ecol.* **46**, 82–91. (doi:10.1111/j.1365-2664.2008.01598.x)
- Fuller, R. M., Smith, G. M., Sanderson, J. M., Hill, R. A. & Thomson, A. G. 2002 Land Cover Map 2000: a general description of the UK's new vector GIS based on classification of remotely sensed data. *Cartographic J.* **39**, 15–25.
- Gaston, K. J., Jackson, S. F., Cantú-Salazar, L. & Cruz-Piñón, G. 2008 The ecological performance of protected areas. *Annu. Rev. Ecol. Evol. Syst.* **39**, 93–113. (doi:10.1146/annurev.ecolsys.39.110707.173529)
- Gibbons, D. W., Reid, J. B. & Chapman, R. A. 1993 *The new atlas of breeding birds in Britain and Ireland, 1988–1991*. London, UK: T. & A.D. Poyser.
- Goldman, R. L., Tallis, H., Kareiva, P. & Daily, G. C. 2008 Field evidence that ecosystem service projects support biodiversity and diversify options. *Proc. Natl Acad. Sci. USA* **105**, 9445–9448. (doi:10.1073/pnas.0800208105)
- Green, R. E., Cornell, S. J., Scharlemann, J. P. W. & Balmford, A. 2005 Farming and the fate of wild nature. *Science* **307**, 550–555. (doi:10.1126/science.1106049)
- Hein, L., van Koppen, K., de Groot, R. S. & van Ierland, E. C. 2006 Spatial scales, stakeholders and the valuation of ecosystem services. *Ecol. Econ.* **57**, 209–228. (doi:10.1016/j.ecolecon.2005.04.005)
- Hörnsten, L. & Fredman, P. 2000 On the distance to recreational forests in Sweden. *Landscape Urban Plann.* **51**, 1–10. (doi:10.1016/S0169-2046(00)00097-9)
- IUCN—The World Conservation Union 1994 *Guidelines for protected area management categories*. Gland, Switzerland: IUCN.
- Jack, B. K., Kousky, C. & Sims, K. R. E. 2008 Designing payments for ecosystem services: lessons from previous experience with incentive-based mechanisms. *Proc. Natl Acad. Sci. USA* **105**, 9465–9470. (doi:10.1073/pnas.0705503104)
- Jackson, S. F. & Gaston, K. J. 2008a Incorporating private lands in conservation planning: protected areas in Britain. *Ecol. Appl.* **168**, 1050–1060.
- Jackson, S. F. & Gaston, K. J. 2008b Land use change and the dependence of national priority species on protected areas. *Glob. Change Biol.* **14**, 2132–2138. (doi:10.1111/j.1365-2486.2008.01628.x)
- Janzen, D. H. 1998 Gardenification of wildland nature and the human footprint. *Science* **279**, 1312–1313. (doi:10.1126/science.279.5355.1312)
- Kareiva, P., Watts, S., McDonald, R. & Boucher, T. 2007 Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science* **316**, 1866–1869. (doi:10.1126/science.1140170)
- Kleijn, D. *et al.* 2006 Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* **9**, 243–254. (doi:10.1111/j.1461-0248.2005.00869.x)
- Loucks, C., Ricketts, T. H., Naidoo, R., Lamoreux, J. & Hoekstra, J. 2008 Explaining the global pattern of protected area coverage, relative importance of vertebrate biodiversity, human activities and agricultural suitability. *J. Biogeogr.* **35**, 1337–1348. (doi:10.1111/j.1365-2699.2008.01899.x)
- Maiorano, L., Falcucci, A. & Boitani, L. 2008 Size-dependent resistance of protected areas to land-use change. *Proc. R. Soc. B* **275**, 1297–1304. (doi:10.1098/rspb.2007.1756)
- Marren, P. 1994 *England's national nature reserves*. London, UK: T. & A.D. Poyser.
- Martin, D. 2007 *Surface Builder Version 1.0*. See <http://www2.geog.soton.ac.uk/users/martindj/davehome/software/surfacebuilder/SurfaceBuilder.zip>.
- McLeod, C. R., Yeo, M., Brown, A. E., Hopkins, J. J. & Way, S. F. 2005 *The Habitats Directive: selection of special areas of conservation in the UK*, 2nd edn. Peterborough, UK: Joint Nature Conservation Committee.
- Millennium Ecosystem Assessment 2005 *Ecosystems and human well-being: synthesis*, Washington, DC: Island Press.
- Milne, R. & Brown, T. A. 1997 Carbon in the vegetation and soils of Great Britain. *J. Environ. Manag.* **49**, 413–433. (doi:10.1006/jema.1995.0118)
- Moilanen, A. *et al.* 2005 Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proc. R. Soc. B* **272**, 1885–1891. (doi:10.1098/rspb.2005.3164)
- Naidoo, R. & Ricketts, T. H. 2006 Mapping the economic costs and benefits of conservation. *PLoS Biol.* **4**, e360. (doi:10.1371/journal.pbio.0040360)
- Naidoo, R. & Iwamura, T. 2007 Global-scale mapping of economic benefits from agricultural lands: implications for conservation priorities. *Biol. Conserv.* **140**, 40–49. (doi:10.1016/j.biocon.2007.07.025)
- Naidoo, R. *et al.* 2008 Global mapping of ecosystem services and conservation priorities. *Proc. Natl Acad. Sci. USA* **105**, 9495–9500. (doi:10.1073/pnas.0707823105)
- National Audit Office 2008 *Natural England's role in improving sites of special scientific interest*. London, UK: The Stationary Office.
- National Statistics 2005 *Population, UK population grows to 59.6 million*. See <http://www.statistics.gov.uk/cci/nugget.asp?id=760>.
- Natural England 2006 *England leisure visits—report of the 2005 survey*. See http://www.countryside.gov.uk/Images/ELVS%20Brochure%20_tcm2-31642.pdf.
- Natural England 2008 *State of the natural environment—Natural England*. See <http://www.naturalengland.org.uk/son/default.htm>.
- Nature Conservancy Council 1989 *Guidelines for the selection of biological SSSIs*. Peterborough, UK: Nature Conservancy Council.
- Nelson, E. *et al.* 2008 Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *Proc. Natl Acad. Sci. USA* **105**, 9471–9476. (doi:10.1073/pnas.0706178105)
- Odling-Smee, L. 2005 Dollars and sense. *Nature* **437**, 614–616. (doi:10.1038/437614a)
- Ricketts, T. H., Daily, G. C., Ehrlich, P. R. & Michener, C. D. 2004 Economic value of tropical forest to coffee production. *Proc. Natl Acad. Sci. USA* **101**, 12579–12582. (doi:10.1073/pnas.0405147101)
- Ricketts, T. H. *et al.* 2008 Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* **11**, 499–515. (doi:10.1111/j.1461-0248.2008.01157.x)

- Russ, G. R., Alcalá, A. C., Maypa, A. P., Calumpong, H. P. & White, A. T. 2004 Marine reserves benefit local fisheries. *Ecol. Appl.* **14**, 597–606. (doi:10.1890/03-5076)
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V. & Woolmer, G. 2002 The human footprint and the last of the wild. *Bioscience* **52**, 891–904. (doi:10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)
- Scott, J. M. *et al.* 2001 Nature reserves: do they capture the full range of America's biological diversity? *Ecol. Appl.* **11**, 999–1007. (doi:10.1890/1051-0761(2001)011[0999:NRDTCT]2.0.CO;2)
- Smallshire, D., Robertson, P. & Thompson, P. 2004 Policy into practice: the development and delivery of agri-environment schemes and supporting advice in England. *Ibis* **146**(Suppl. 2), 250–258.
- Stroud, D. A. *et al.* 2001 *The UK SPA network: its scope and content. Volume 1: rationale for the selection of sites.* Peterborough, UK: Joint Nature Conservation Committee.
- Sutherland, W. J. *et al.* 2006 The identification of the 100 ecological questions of high policy relevance in the UK. *J. Appl. Ecol.* **43**, 617–627. (doi:10.1111/j.1365-2664.2006.01188.x)
- Turner, W. R. *et al.* 2007 Global conservation of biodiversity and ecosystem services. *Bioscience* **57**, 868–873. (doi:10.1641/B571009)
- United States Department of Agriculture 2008 *Conservation reserve program: summary and enrolment statistics.* See http://www.fsa.usda.gov/Internet/FSA_File/annual_consv_2007.pdf.
- Xue, D. & Tisdell, C. 2001 Valuing ecological functions of biodiversity in Changbaishan Mountain Biosphere Reserve in Northeast China. *Biodivers. Conserv.* **10**, 467–481. (doi:10.1023/A:1016630825913)