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Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity

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Summary

1. Understanding and quantifying constraints to multiple ecosystem service delivery and biodiversity is vital for developing management strategies for current and future human well-being. A particular challenge is to reconcile demand for increased food production with provision of other ecosystem services and biodiversity.

2. Using a spatially extensive database (covering Great Britain) of co-located biophysical measurements (collected in the Countryside Survey), we explore relationships between ecosystem service indicators and biodiversity across a temperate ecosystem productivity gradient.

3. Each service indicator has an individual response curve demonstrating that simultaneous analysis of multiple ecosystem services is essential for optimal service management. The shape of the response curve can be used to indicate whether 'land sharing' (provision of multiple services from the same land parcel) or 'land sparing' (single service prioritisation) is the most appropriate option.

4. Soil carbon storage and above-ground net primary production indicators were found to define opposing ends of a primary gradient in service provision. Biodiversity and water quality indicators were highest at intermediate levels of both factors, consistent with a unimodal relationship along a productivity gradient.

5. Positive relationships occurred between multiple components of biodiversity, measured as taxon richness of all plants, bee and butterfly nectar plants, soil invertebrates and freshwater macroinvertebrates, indicating potential for

management measures directed at one aspect of biodiversity to deliver wider ecosystem biodiversity.

6. We demonstrate that in temperate, human-dominated landscapes, ecosystem services are highly constrained by a fundamental productivity gradient. There are immediate trade-offs between productivity and soil carbon storage but potential synergies with services with different shaped relationships to production.

7. *Synthesis and applications*. Using techniques such as response curves to analyse multiple service interactions can inform the development of Spatial Decision Support tools and landscape-scale ecosystem service management options. At intermediate productivity 'land-sharing' would optimise multiple services, however, to deliver significant soil carbon storage ‘land-sparing’ is required i.e. resources focused in low productivity areas with high carbon to maximise investment return. This study emphasises that targets for services per unit area need to be set within the context of the national gradients reported here to ensure best use of limited resources.

Keywords: **Countryside Survey, trade-offs, landscape, soil carbon, water quality, pollination, productivity**

Introduction

Increasing pressures on natural resources, the depletion of natural capital and concerns about the impacts of environmental change have led to a new research and policy agenda based on the concept of ecosystem services (Kremen & Ostfeld 2005; MA 2005. The strength of the ecosystem service concept is that it brings together multiple elements that interact within a landscape and fosters recognition and valuation of the goods that ecosystems provide. The ecosystem service potential of a landscape is a function of ecosystem properties and anthropogenic pressures that can promote or degrade service delivery (Mooney 2010). Understanding and predicting how multiple ecosystem services co-vary, particularly in relation to drivers of change, is a research imperative for guiding sustainable environmental management for human well-being (Bennett, Peterson & Gordon 2009; Raudsepp-Hearne *et al.* 2010). Ecosystems that are associated with inherently different levels of productivity and disturbance may respond differently to the same anthropogenic stressors (Wright & Jones 2004). Anthropogenic impacts may simultaneously enhance multiple ecosystem services, alternatively attempts to maximise one service may result in the loss of other services (trade-offs). Trade-offs between services may be inevitable but would be better made as informed choices rather than unforeseen side-effects (Rodriguez *et al.* 2006). Patterns of co-variation between services may not be linear; they may be unimodal or have thresholds or tipping points.

Biodiversity is assumed to be critical to the provision of ecosystem services (MA 2005), although an understanding of the quantitative links between biodiversity and individual ecosystem services is incomplete (Kremen 2005; Isbell *et al*. 2011). Taxonomic or trait-based subsets of biodiversity directly provide goods and services (e.g. wild species diversity (Norris *et al.* 2011)) as well as underpinning fundamental ecosystem processes required to deliver ecosystem services (e.g. net primary production). The contribution of biodiversity to service provision includes the presence of particular species and traits (Luck *et al.* 2009) and potentially, resilience through functional diversity and redundancy of species and traits within the ecosystem (Mace *et al.* 2012).

Defining fundamental evidence-based relationships to help determine land management strategies has been limited by a lack of large-scale quantitative analyses of the distribution of ecosystem services and the interactions between them (Balvanera *et al.* 2001). There are probably two reasons for this: First, a lack of data collected at sufficiently fine resolutions across representative landscapes. Few studies have quantified the impact of multiple drivers across landscapes, of a range of ecosystem services and biodiversity measures. Ideally this would comprise co-located, fine-grained data to measure relationships between services delivered by specific habitats. Such data are costly and scarce, but are necessary to unpick how changes in ecosystem service supply are subject to global change drivers and national or regional policies whose impacts cross ecosystem boundaries. Lack of data at this scale usually necessitates averaging over large grid cells and using data sampled at different temporal and spatial scales (Naidoo *et al.* 2008; Anderson *et al.* 2009). However, averaging biodiversity confounds alpha with beta diversity leading to a false or incomplete impression of the contribution of ‘within habitat’ versus ‘among habitat’ diversity to ecosystem service provision (Huston 1999, Whittaker *et al*., 2001, Eigenbrod *et al*., 2010). Many studies have used pairwise comparisons of ecosystem services (Naidoo *et al*., 2008, Anderson *et al*. 2009), although useful, it is necessary to move beyond this and analyse multiple service interactions in relation to ecological space. In order to plan for mixed service delivery, a unifying framework for understanding the wider ecological constraints on local relationships is needed.

Second, a lack of correspondence between basic biophysical measurements and ecosystem services. Some biophysical measurements can directly represent the supply side of a final ecosystem service (explicitly linked to goods provided by ecosystems). In other cases, measurements may represent an intermediate service or process, which provide essential support for final services but cannot be directly linked to consumption (Mace *et al.* 2011). To quantify ecosystem service delivery effectively it is essential to identify specific biophysical measurements which can be used directly or translated into indicators of ecosystem service supply. These are separate from the demand-side that is in turn quantifiable by metrics related to social and economic behaviours and the locations of human populations. This paper focuses on supply rather than demand. To clearly characterise pathways of ecosystem service production and consumption, consistency and transparency is needed in defining ecosystem services and the biophysical measures used to represent them. This requires consensus between land users, policy makers and researchers regarding the relevance and appropriateness of derived measures (Haines-Young, 2011).

Here we exploit a uniquely large-scale but fine-grained dataset of ecosystem service indicators to quantify the limits of the ecological space in which biodiversity and ecosystem services co-vary. This dataset spans the temperate landscape of Great Britain which has a long history of human settlement and agricultural exploitation. Our overarching hypothesis is that the potential for delivering multiple services across mosaics of ecosystems is fundamentally constrained by a large-scale ecosystem productivity gradient (Huston & Wolverton 2009), which in turn has a predictable relationship with aquatic and terrestrial above- and below-ground biodiversity (Loreau *et al.* 2001; Zavaleta *et al.* 2010). If this holds true, quantifying these cross-ecosystem relationships will provide the basis for a predictive framework for landscape managers indicating the extent to which different services could be jointly maximised given average productivity in a temperate region of interest; a 'land-sharing' or 'land sparing' approach (Green *et al*., 2005).

Materials and Methods

We used data from a Great Britain (GB) wide surveillance dataset, the Countryside Survey (CS) 2007, to quantify the relationships between multiple ecosystem service indicators and biodiversity across all major ecosystem types. CS 2007 is a unique dataset sampling a series of 1x1 km squares across Britain (Fig. 1) to record ecological attributes and land use change in great detail over time (http://www.countrysidesurvey.org.uk). The sample design is based on a series of stratified, randomly selected 1-km squares, which numbered 591 in the 2007 survey. Stratification of sample squares was based on a classification of all 1-km squares in Britain using their topographic, climatic and geological attributes obtained from published maps (Bunce *et al.* 1996). Within each 1-km square, plants and soils were sampled within randomly selected co-located plots, freshwater samples were taken from headwater streams, and landuse and habitat information was collected for all of the land parcels within the 1-km square.

Translating biophysical measurements to ecosystem service indicators

The biophysical measurements recorded in CS were translated into ecosystem service indicators in consultation with an expert group of scientists and policy-makers. The research team derived a draft set of relationships, some based on trait-based ecosystem service proxies (which are increasingly being used in ecosystem service studies (Lavorel *et al.* 2011, Diaz *et al.*2007)). These were then refined in a series of workshops comprising experts from the academic sector, Non-governmental organisations and government agencies (Natural England, Defra, Countryside Council for Wales, Scottish Natural Heritage). Consensus was reached after discussions with a specially convened group of experts who acted as a steering group for the project. An ecosystem service cascade, defining measurement, service, function and pressures (see Fig. S1 in Supporting Information, Haines-Young & Potschin (2007)) was completed for each biophysical measurement. The use of stakeholders to relate local or regional ecosystem services to ecosystem properties and indicators has precedent (Quetier *et al.* 2007. Lavorel *et al.* 2011), our consultation exercise was targeted at the national scale and stakeholders involved in national policy development. This resulted in an agreed series of ecosystem service indicators (Table 1) (Smart *et al.* 2010a). The scale at which the data was collected is presented for each indicator, since different ecosystem compartments required sampling at different spatial scales, for example, freshwater biodiversity measurements were based on one assessment in the headwater stream within each 1-km square. Analysis was carried out by averaging ecosystem service indicators across 1-km squares and also by analysing plot-level observations within and between squares.

The Ecosystem Service indicators

We used taxon richness and community composition measures to quantify various components of biodiversity. Subsets of specific taxa were used as indicators of the potential for supply of different ecosystem services across the landscape mosaics sampled by each 1-km square. For example, stream macroinvertebrate community metrics reflect established relationships between diversity and water quality (Clarke et al 2008). In addition, terrestrial biodiversity indicators were constructed from plant species compositional data recorded from five random 200-m^2 plots in each 1-km square as follows: the richness of nectar providing plants for bees and butterflies, (Carvell et al 2006), was used as an indicator of the regulating service of pollination. Studies have demonstrated the importance of wild pollinators and the availability of pollinator habitat to wild flower production (Biesmeijer *et al.* 2006) and crop productivity (fruit set) (Garibaldi *et al.*, 2011). Indicators of biodiversity include terrestrial plant species diversity (measured as total taxon richness of plant species in 200-m^2 vegetation plots) (Smart *et al.* 2003), soil invertebrate diversity (measured as total taxon richness in 8-cm depth soil samples) and freshwater biodiversity (measured as an index combining species richness and rarity; the Community Conservation Index (CCI) (Chadd & Extence 2004).

Freshwater macro-invertebrate samples from headwater streams were used to calculate the observed/expected average BMWP (Biological Monitoring Working Party) score per Taxon (ASPT) (Armitage *et al.* 1983): an indicator of biological water quality.

Soil carbon storage was quantified as loss-on-ignition for the top 15cm of soil (Emmett *et al.* 2010) from soil samples co-located with the five random vegetation sampling plots in each 1-km square.

The cultural service indicator 'Charismatic Landscapes' was calculated from CS habitat mapping data based on area of woodlands, water, sea, altitude and relief (measured as the cover of particular habitat types and land elevation). High values of these landscape attributes are associated with more highly preferred landscapes in Britain (Norton *et al*. 2012).

Cover-weighted Specific Leaf Area (cSLA) (a weighted average of plant species cover in the 200-m^2 plots) was used as a correlate of above-ground net primary productivity (ANPP) (Garnier *et al.* 2004). Specific Leaf Area (SLA) data were extracted from Grime *et al.* (1995) and the LEDA database (Kleyer *et al.* 2008).

These indicators together are assumed to be correlated with the delivery of a suite of final provisioning (food and fresh water), regulating and cultural services following the Millennium Ecosystem Assessment (MA 2005) nomenclature, the more recent UK National Ecosystem assessment (Mace *et al.* 2011) and supported by the results of the expert and stakeholder consultation. Maps of the average CS 1-km square level value for each ecosystem service indicator are shown in Fig. S2. Pairwise plots and correlations of the raw data are shown in Fig. S3.

Analyses at 1-km square resolution

Multivariate analyses of the spatial relationships between ecosystem service indicators and explanatory variables (e.g. climate, soil pH, amount of intensive land) were undertaken using Canoco (ter Braak & Smilauer 2002). Data were collated at the 1-km square resolution, and all variables were centred and standardised and analysed as mean and standard deviations of ecosystem service indicator values per square.

A series of analyses were carried out which tested the hypothesis that the multivariate set of ecosystem service indicator variables co-vary predictably along a primary axis interpretable as a cross-ecosystem productivity gradient. First, to determine the major axes of variation in the data an unconstrained ordination was carried out using Principal Components Analysis (PCA). This provided an ordination space within which individual indicator variables were projected allowing quantification of the covariance between axis 1, the two primary productivity related indicator variables; cSLA and soil carbon content, and the other biodiversity and cultural indicators. Then, to better visualise the response of each indicator variable, semi-parametric Generalised Additive Model (GAM) curves were constructed based on the first PCA axis as the sole explanatory variable. These are simple univariate models allowing for smoothly varying relationships between the response (the ecosystem service indicator variable in question) and the predictor (the first PCA axis). This enables a clear visualisation of the relationship between each indicator variable and the primary ordination axis derived from the covariance between all indicator variables.

The unconstrained ordination analysis was repeated but included the standard deviations of each variable per square (where based on replicate measurements within each square). This analysis was carried out to test the hypothesis that maximum variability in indicator variables within each square would coincide with 1-km squares of intermediate mean productivity. Simpson's evenness index is commonly used for assessing landscape diversity (Smith & Bastow-Wilson, 1996); it is not sensitive to rare low cover habitats. It was calculated to express the diversity and area distribution of habitats in each 1-km square and was passively added to this ordination to test whether variation in ecosystem service indicators was positively related to habitat diversity.

Redundancy Analysis (RDA) was then used to test the explanatory power of independent predictors of productivity against the principal axis in the unconstrained ordination.

Assembly of explanatory variables

We assembled covariates that together represent the major controls (soil, climate and land-use) on primary productivity across terrestrial ecosystems (Huston & Wolverton 2009). Land use was measured as the percentage of the 1-km square covered by arable plus intensive grassland (Carey *et al.* 2008). Climate variables included mean annual rainfall and mean annual temperature. Long-term annual average data for the period 1978 to 2005 were extracted from the UK Met Office 5x5 km gridded data archive at www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09. Soil pH was measured on a homogenised sample from the top 15cm of soil in each of the five random 200-m^2 plots in each CS square (Emmett *et al.* 2010).

The process model JULES was used to generate an independent estimate of ANPP (Kg C ha^{-1}) for each 1-km square for 2006, the year preceding the field survey. JULES is a process-based model that simulates the fluxes of carbon, water and energy between the atmosphere and the land surface. We used a configuration of JULES version 2.2 (Best *et al.* 2011; Clark *et al.* 2011) including a two-stream, multi-layer model of radiation interception by the canopy, with photosynthesis calculated separately for sunlit and shaded leaves. JULES was driven by daily meteorological data for the period 1971 to

2007. The dominant soil type for each 1-km square was used to calculate the hydraulic and thermal characteristics of the soil. The fraction of each land cover type in a 1-km square was estimated using CS data employing a static map of land cover for each square based on the 2007 survey and translating these into cover of one of eight land surface types.

In addition, a map of the residuals was created (Fig. S3) by subtracting the unconstrained axis 1 scores from the axis scores constrained by all productivity-related covariates. There were no apparent spatial trends suggesting that the unconstrained axis was not influenced by unknown predictors aligned along geographic gradients.

Analyses at a finer resolution (sample plots within each 1-km square)

Analysis of the interrelationships between pairs of service indicators was undertaken in SAS (proc mixed, Singer 1998) using a much larger dataset including plot level data to improve the spatial resolution where possible. A mixed model analysis of variance was used, incorporating the CS 1-km square as a random effect to account for the non-independence of plots located within the same square. Degrees of freedom were calculated using the approximation of Satterthwaite (1946). Given the plausibility of a humpbacked relationship between productivity and species diversity (Grime 1973), a quadratic model was also tested.

Results

The relationships between ecosystem service indicators showed clear patterns of covariance but each indicator had a unique response curve (Fig 2 and Table 2). Soil carbon and cSLA occupied opposing ends of the unconstrained first ordination axis.

This supports the hypothesis that the principal axis along which the indicators co-vary is strongly correlated with primary productivity. Soil biota, freshwater invertebrate and plant species diversity all exhibited unimodal relationships along the principal axis with the highest biodiversity occurring toward the centre of the first axis (Fig. 2 and Table 2). Biological water quality and butterfly nectar plant richness were highest at intermediate positions on the inferred productivity gradient (Fig 2). Water quality declined at high productivity and declined slightly at high soil carbon. Butterfly nectar plant diversity was positively related to soil carbon and bee nectar plant diversity was unimodally related to soil carbon. Positive covariance was found between all components of biodiversity, plant species diversity (including bee and butterfly nectar plants) and soil and freshwater invertebrate diversity (Fig. 2 and Table 2). Overall the unconstrained first axis explained 35% of the joint variation among indicator variables (Table 3).

The relationships between ecosystem service indicators and the principal axis when constrained by soil pH, land-use, climate or the process-based model estimates of ANPP are shown in Fig. 4. Figure 4a demonstrates the expected positive covariance between modelled ANPP and cSLA and negative covariance with soil carbon. This is consistent with higher primary production being associated with high SLA species with higher tissue N content and higher decomposability as opposed to low productivity sites, where litter inputs from low SLA species in cool, high-rainfall areas are also associated with peat accumulation and the highest values of soil carbon content. Despite the consistency of the relationship, JULES ANPP estimates only explained 9.9 % of the constrained ordination axis (Fig4a, Table 3). Larger amounts of variation were explained by land use intensity, soil pH and climate (Table 3 and Fig 4b, c, d). Intercorrelation between all these covariates leads to a total explanatory power for the unconstrained principle axis of less than their sum (74.7%, Table 3).

When the principal axis was constrained by land-use intensity (Fig. 4b) relationships with ecosystem service indicators closely resembled those depicted in the unconstrained ordination (Fig 2b). High values of cSLA were associated with a greater proportion of intensive land use per 1-km square but, apart from the cultural indicator, all other ecosystem service indicators declined as land-use intensity increased (Fig 4b).

A positive relationship was found between rainfall and soil carbon storage, plant diversity and water quality (mean annual temperature showed similar but opposite relationships i.e. higher temperatures associated with higher cSLA) (Fig 4.c). Soil pH (Fig. 4d) produced a very similar set of curves to intensive land (Fig. 4b) demonstrating that the area of intensive land use tends to increase alongside average soil pH.

High habitat diversity within 1-km squares broadly coincided with the middle of the principal ordination axis close to optima for indicators with hump-backed response curves including soil diversity, freshwater diversity and plant diversity (Fig 2b). High habitat diversity also tended to coincide with the highest within-square standard deviations of plant diversity, cover-weighted Specific Leaf Area and soil invertebrate diversity (Fig 3). The highest variation in soil carbon was associated with the highest variation in other biodiversity and service indicators (Fig 3).

Discussion

Our results show that large-scale, yet finely resolved data based on co-located multiple biophysical measures can be used to define the ecological space within which ecosystem service indicators and biodiversity co-vary. This has direct implications for the development of management strategies appropriate to the ecosystem services and biodiversity present in different parts of the landscape.

Ecological constraints on service provision

Our results are applicable to ecosystem mosaics in the temperate zone and show how the delivery of multiple ecosystem services and relationships with biodiversity are likely to be constrained by underlying ecological conditions. Plant, soil and freshwater biodiversity indicators conveyed a unimodal pattern along this principal gradient. Similar unimodal relationships between biodiversity and productivity have been observed in temperate plant communities (Grime 1973; Al-Mufti *et al.* 1977; Zobel & Partel 2008) but not at the scale and resolution of this dataset or including relationships with soil and water data. However, because we averaged diversity across samples within a 1-km square, a proportion of this variation was due to species compositional turnover and abiotic variation between habitats.

Maximum levels of provisioning services, associated with high values of the ANPP indicator, co-occurred with low levels of regulating services, such as water quality (Raudsepp-Hearne *et al.* 2010). The decline in biological water quality associated with increasing intensive land-use (and high ANPP) found in this study is well documented elsewhere (Allan 2004). Although such trade-offs between services and productivity might be expected (Eigenbrod *et al.* 2009; Raudsepp-Hearne *et al.* 2010), the low service levels associated with high productivity are of concern both for service provision across a landscape and because long-term ecosystem sustainability relies on the maintenance of supporting and regulating services (Raudsepp-Hearne *et al.* 2010).

The highest levels of biodiversity occurred with intermediate levels of soil carbon. Other studies have identified a positive relationship between biodiversity and carbon storage, finding for example, positive covariance between biodiversity and carbon in tropical regions (Strassburg *et al.* 2010). Heavily human-impacted temperate regions such as the UK show different patterns of carbon storage (Anderson *et al.* 2009). Soil carbon in Great Britain is highest in colder, wetter climates, mostly upland environments. Such conditions, which inhibit decomposition and promote build-up of soil carbon, are known to be associated with habitats with low ANPP, i.e. typified by slow-growing plant species with low SLA and reduced alpha (within habitat) diversity as a result of species pool filtering by abiotic extremes (Smart *et al.* 2010b). Although taxon richness is typically low, these ecosystems contribute to wider regional gamma diversity by providing niche space for specialised biota often of conservation concern, either culturally important or essential to ecosystem function.

At the extremes of soil carbon storage (low and high) we predict that increasing other ecosystem services to sustainable levels will be much more difficult than in regions where average soil carbon levels are intermediate. In the latter, options to jointly maximise biodiversity and other ecosystem services are predicted to be possible but carbon concentration per unit area of soil will still be low relative to the maximum observed in peatland ecosystems.

Relationships between biodiversity components

Previous evidence for large-scale positive spatial covariance in the diversity of different taxonomic groups varies (Billeter *et al.* 2008).We found positive covariance between all biodiversity indicators measured across the temperate ecosystems of Britain. This suggests that policy directed towards stewardship of the diversity of one component could benefit other types of diversity. Since high biodiversity is likely to reflect the lack of conversion of mosaics of semi-natural ecosystems, this also emphasises the importance of ongoing habitat protection. Biodiversity monitoring is often based on charismatic or easily identifiable taxonomic groups (Norris *et al.* 2011) but these may have little direct relationship to ecosystem function. Indicators that demonstrate the role that biodiversity plays in underpinning ecosystem services are more difficult to define because there is still a poor understanding of which species are important for ecosystem functioning and maintenance of ecosystem services (Luck *et al*., 2009).

Land management for service provision

Our analysis has the potential to help inform future land management options to optimise mixed ecosystem service supply. To date, options have tended to focus on protection of areas of high species diversity (Rands *et al.* 2010), or on single ecosystem services such as climate regulation by carbon sequestration (Strassburg *et al.* 2010). New strategies for the protection of multiple ecosystem services are likely to be necessary, consistent with the rising popularity of an ecosystem approach to spatial planning and land management (Goldman *et al.* 2008).

Within-square variation in most ecosystem service indicators was positively correlated with habitat diversity (Fig. 2b, 3). Both tended to be highest towards the centre of the productivity axis where biodiversity indicators also attained maximum values. This indicates the importance of variation in habitat types (heterogeneity) and associated land use in optimising a range of indicators at the 1-km square scale (Benton, Vickery & Wilson 2003). The coincidence between high habitat diversity, high biodiversity indicator values and intermediate productivity also suggests that the intensity of management across the mix of habitats that make up the within-square mosaic is important. High productivity, for example, should be accompanied by low productivity in other areas yet, because of fundamental soil and climate constraints, the landscape scale ordination predicts a limit on the range of productivity values that can be sustained in any 1-km square. Thus the very highest productivity is rarely found in close proximity to the very lowest values. The challenge is therefore to identify management approaches that acknowledge the opportunities and constraints associated with the position of any one location on the productivity gradient.

The concept of land-sharing vs. land-sparing offers a potentially useful approach for spatial planning of service provision and impacts on biodiversity (Green *et al.* 2005). Coupling the approach with our results, the yield/population density curves in the original model are substituted for ecosystem service response curves from the unifying ordination space (Fig. 5). Land sharing can then be considered as a multi-functional approach to land use where delivery across multiple ecosystem services is prioritised. Introducing habitat heterogeneity and providing refuges for species are attempts to retain services such as pollination and water quality, plus biodiversity where otherwise they would be lost to food production (Whittingham 2011). However, this may mean that there is a cost in production (yield), resulting in the need for larger areas to be farmed to maintain both yield targets and other ecosystem services. An alternative is 'land sparing' which spatially segregates land areas devoted solely to production from areas prioritised for other ecosystem services, according to suitability. In Fig. 5, the black dotted line signifies the optimal service response. For curve a, the level of service drops off rapidly with production so land sharing is not a viable option. Curve b depicts a more resistant ecosystem service since supply stays at a higher than average level as production increases so there would be potential for land sharing. If this concept were applied to the graph between intensive land and service indicators (Fig. 4b), soil carbon storage would be an example of where a land sparing policy should be applied as there is a sharp decline in soil carbon with intensity of land use. This method could provide guidance on expected levels of multiple ecosystem services at different positions along the productivity gradient thus helping identify priorities for management in multi-functional landscapes. As planning for ecosystem service provision takes place at different spatial scales from farm to catchment, to region to national, the next challenge is to disaggregate the data to determine the stability of the relationships at these different scales and to explore contextual dependencies which may limit or enhance final service delivery, including demand, consumption and the realisation of human benefits.

Conclusion

Our analyses demonstrate how multiple ecosystem service indicators trade-off against one another along a landscape scale primary productivity gradient. The use of response curves, in particular, is recommended as a method to assess the potential for synergies or trade-offs amongst services. Covariance among service indicators suggests it is impossible to simultaneously achieve maximum levels of biodiversity indicators and either primary production or soil carbon storage. The greatest potential for jointly maximising biodiversity alongside other ecosystem service indicators is at intermediate productivity and this may be partly realisable by high habitat diversity.

This kind of evidence provides a vital landscape-scale context for those making decisions about strategies for optimising ecosystem service delivery. For example, at a national scale, maintaining and protecting areas of high carbon storage (‘land sparing’) is essential in order to balance low carbon storage in areas more suited to the delivery of multiple ecosystem services (‘land sharing’). Similarly, such contextual information helps to manage expectations about the likely return among other ecosystem services within areas most suitable for food and fibre production.

Our quantification of this trade-off space could be readily incorporated into decision support tools to foster better spatial planning of ecosystem service supply.

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Additional information Data and reports are available from the Countryside Survey website (http://www.countrysidesurvey.org.uk/).

Supporting information

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

Fig. S1: The ecosystem service cascade taken from Haines-Young & Potschin (2007)

Fig S2. Distribution maps of each of the ecosystem service indicator variables used in the analysis for Figures 2, 3, 4.

Figure S3: Correlation plots of paired ecosystem indicators from raw data used for ordination analyses.

Fig. S4: Map of residuals resulting from subtracting unconstrained ordination axis 1 scores from scores constrained by potential explanatory variables.

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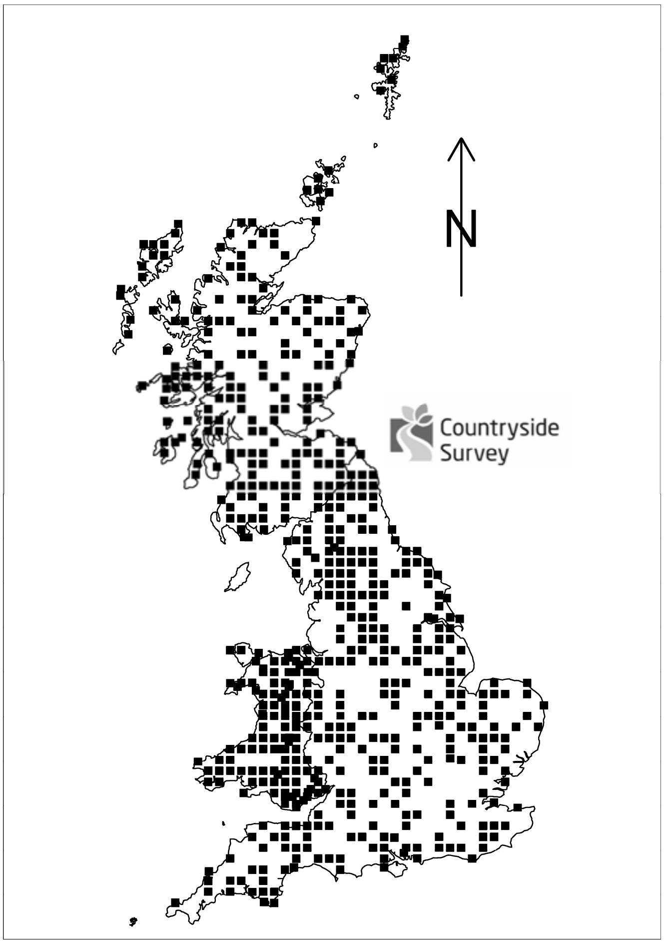

Fig. 1: The distribution of CS squares across Great Britain (GB).

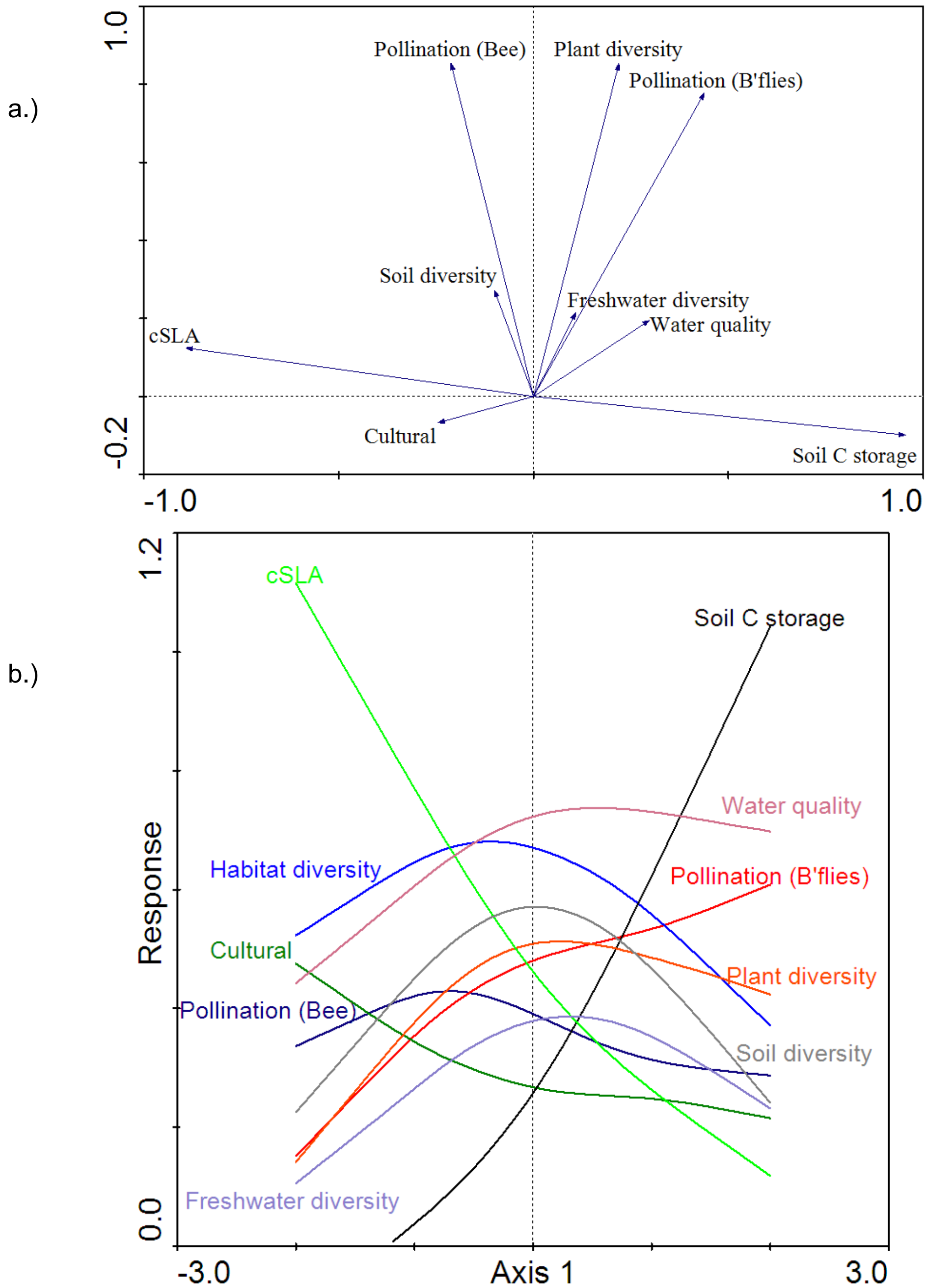

Fig. 2: Relationships between ecosystem service indicators, a.) Multi-variate analysis (Principle Components Analysis) of ecosystem service indicators across 1km CS squares b.) Response curves of ecosystem service indicators along first ordination axis (fitted using Generalised Additive Models).

(ecosystem service indicators; plant diversity (richness in a 200-m^2 plot), Pollination (Bee) and Pollination (B'flies) (richness of Bee and Butterfly nectar plants in a 200-m^2 plot), soil diversity (total taxon richness of soil invertebrates from 15-cm soil cores co-located with each 200-m^2 vegetation plot), Soil carbon storage (Loss-On-Ignition), Freshwater diversity (freshwater macro-invertebrate diversity-CCI index), Water quality (biological measurement), cSLA (mean cover-weighted Specific Leaf Area; trait-based indicator of ANPP), Habitat diversity (Simpson's index, added as a passive variable)

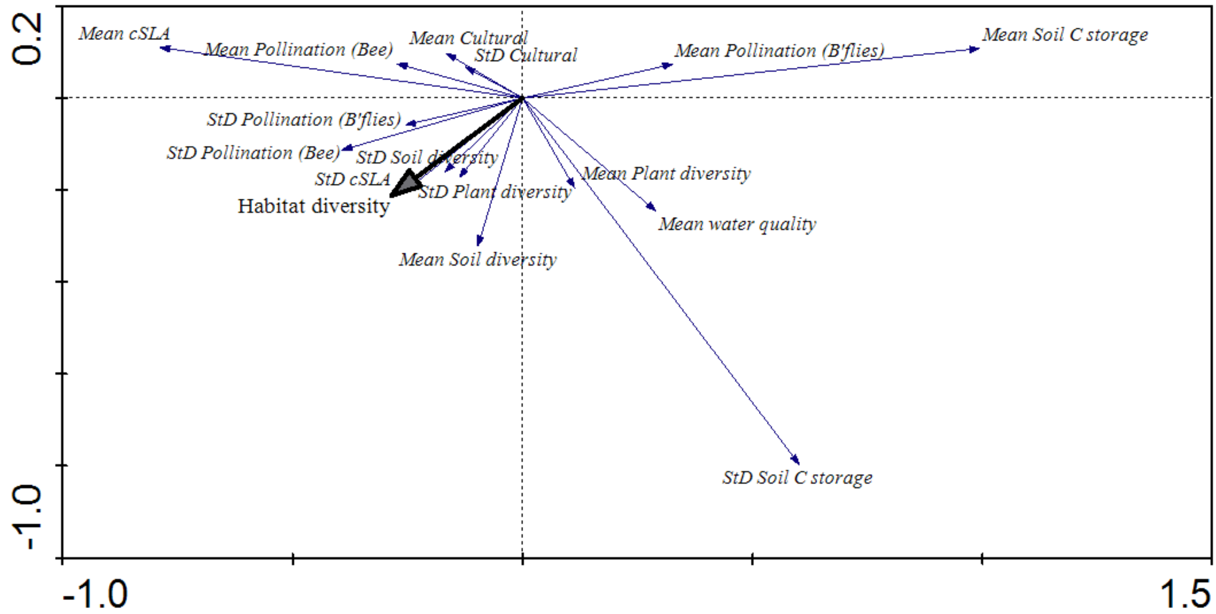

Fig. 3: Multi-variate analysis (PCA) of ecosystem service indicators including standardised mean values of services and their standard deviations (SD). Habitat diversity per 1-km square (Simpson's index) has been added passively to the ordination.

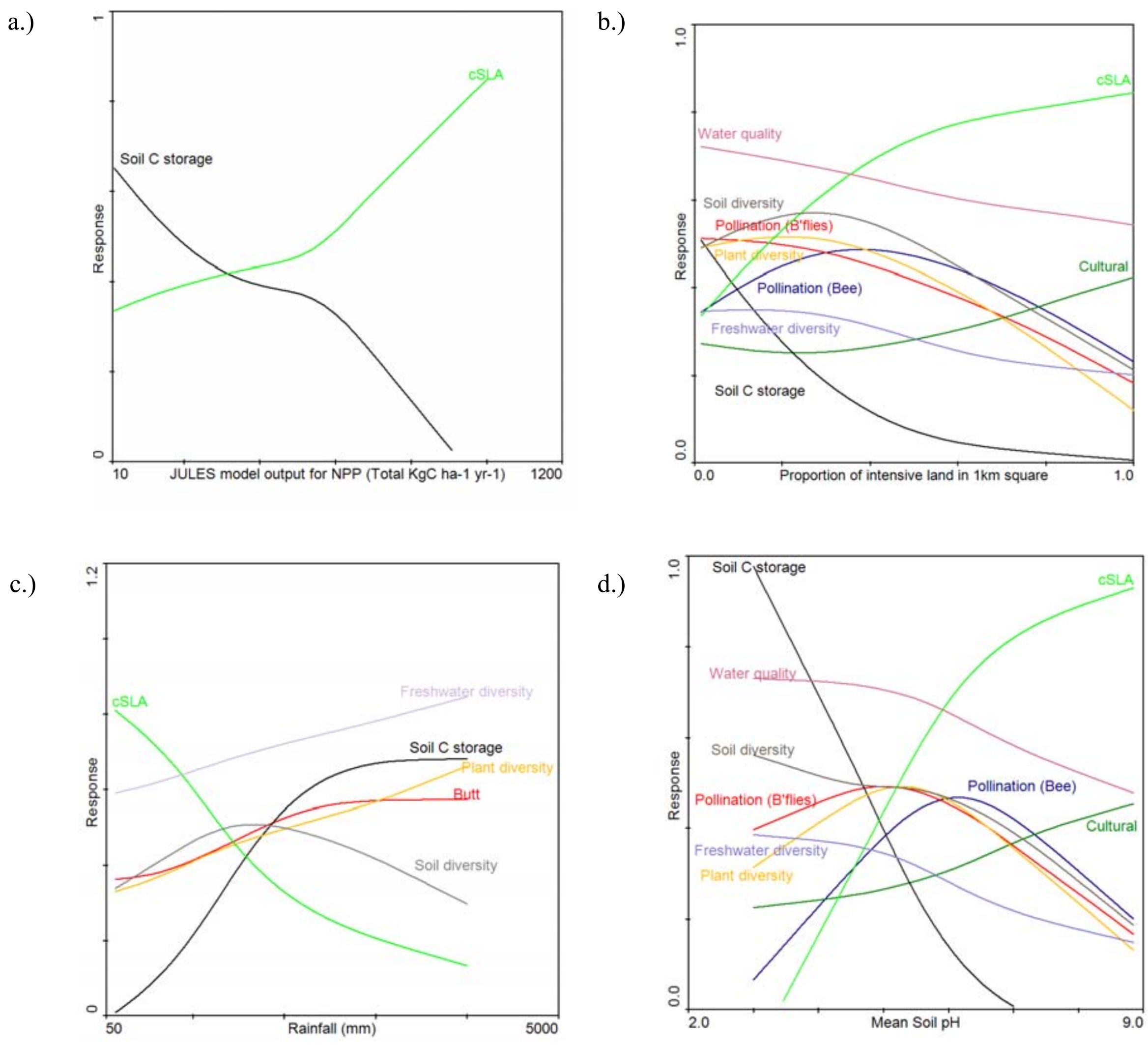

Fig. 4: Response curves of mean ecosystem service indicators per 1-km^2 across Great Britain, fitted using Generalised Additive Models to ordination axes constrained by; a.) modelled average annual NPP from the JULES model b.) proportion of intensive land (Arable and Improved grassland habitats) within each 1-km square from CS field survey data c.) mean long-term annual average rainfall (1978–2005) and d.) mean soil pH from five random sampling locations in each 1-km square. All X axes are scaled to the units of each constraining variable.

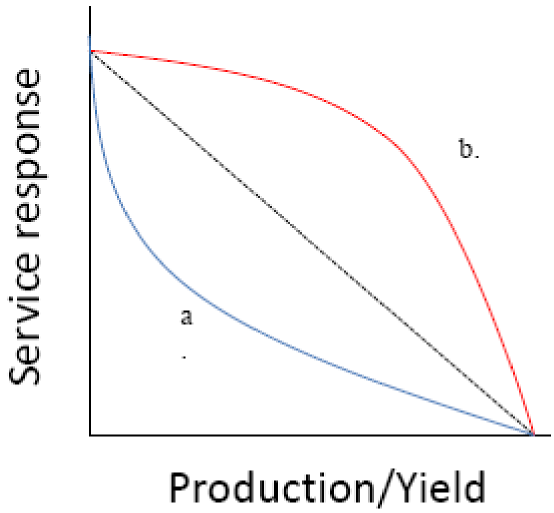

Fig. 5: Conceptual diagram showing hypothetical responses of ecosystem services to production intensity. The black dashed line indicates optimal service response. Curve a (blue line) shows a sharp decline in service response with productivity so land-sparing would be favoured for this service. Curve b (red line) shows that the service maintains a higher than expected service level with increasing productivity and there is some capacity for land sharing.

Ecosystem compartment	Biophysical measurement	Ecosystem process or Intermediate Ecosystem service	Final Service	Evidence for link between metric and service	Comments on link between biophysical measurements and services	Scale
Headwater streams	Average Score per Taxon for macroinvertebrates	Water quality	**Clean water provision**	4	Freshwater macro-invertebrates have been well studied as indicators of freshwater quality	stream stretch (~20m)
Headwater streams	CCI Index for macroinvertebrates	Freshwater Biodiversity, (Nutrient cycling)	**Clean water provision**	4	Reflects an aggregate conservation value of a macro-invertebrate sample	stream stretch (~20m)
Soil	Soil invertebrate taxa diversity	Soil Biodiversity, (Nutrient cycling)	**Soil purification, Provisioning**	2/3	Various papers indicate importance of soil biota for plant growth and contaminant removal	soil core (0-8cm)
Soil	Carbon storage LOI	Soil Carbon storage	**Climate regulation**	4	Soils well accepted as important global carbon store	soil core (0-15cm)
Plants	Total plant taxon diversity	Plant Biodiversity,	**Wild species diversity, (Provisioning, Cultural)**	4	Total species pool in each plot from which subsets of other culturally significant or functionally important taxa and traits are drawn. Sometimes imprecisely equated with a measure of resilience.	vegetation plots ($200m^2$)
Plants	Bee nectar sources	Pollination, (Biodiversity)	**Pollination, (Provisioning, Wild species diversity)**	4	Measures diversity of nectar-providing plants (changes have been correlated with changes in wild bee diversity in NW Europe). The link with crop pollination is correlative but focuses on a functionally critical component of pollinator foodwebs.	vegetation plots ($200m^2$)
Plants	Butterfly nectar sources	Pollination, (Biodiversity)	**Pollination, (Wild species diversity; Cultural)**	4	Less important as contributor to fruit set and crop productivity but important for maintenance of wild butterfly diversity	vegetation plots ($200m^2$)
Plants	Specific Leaf Area	Above-ground NPP	**Provisioning**	4	Based on the positive correlation between ANPP and the abundance-weighted trait within each plant assemblage.	vegetation plots ($200m^2$)
Landscape	Water, trees, coast, altitude and relief	Charismatic landscapes-Cultural	**Cultural**	3	Collaboration with researchers for Natural England who found that areas of woodland, water, coastline and altitudinal variation enhanced people's cultural experience of a landscape	$1km^2$

Table 1: Ecosystem service indicators used in the analyses with the corresponding biophysical variables measured in Countryside Survey. Evidence index: 1 = low agreement, limited evidence; 2 = low agreement much evidence; 3= high agreement limited evidence; 4=high agreement, much evidence

	Soil invertebrate diversity (N=921)	Freshwater invertebrate diversity (N=701)	Bee nectar plants (N=2675)	Butterfly nectar plants (N=2675)	Water quality (N=701)	Soil Carbon (N=2620)	cSLA (N=2579)	Cultural (N=2679)
Plant species richness	+ 0.002	+ <0.001	+ <0.001	+ <0.001	+ <0.001	Unimodal <0.001	Unimodal <0.001	+ <0.001
Soil invertebrate diversity		+ 0.009	+ 0.002	+ 0.001	+ 0.02	Unimodal <0.001	ns	+ <0.001
Freshwater Invertebrate diversity			ns	+ 0.03	+ <0.001	ns	- <0.001	+ <0.001
Bee nectar plants				+ <0.001	ns	Unimodal <0.001	Unimodal <0.001	+ <0.001
Butterfly nectar plants					+ 0.002	+ <0.001	Unimodal <0.001	+ <0.001
Water quality						Unimodal <0.001	- <0.001	+ <0.001
Carbon storage (soil)							- <0.001	+ <0.001
cSLA								- <0.001

Table 2: Correlations between service indicators using a mixed model analysis of variance. *P*-values and direction of change are shown. A larger dataset was used for these analyses than those in Figures 2, 3 and 4

Variable	Variation explained	F	P
Unconstrained axis 1	35.4%	na	na
All constraining variables	27.4 (74.7) %	na	na
JULES NPP	3.4 (9.9) %	3.87	0.006
Climate			
Rainfall	12.9 (35.2) %	16.48	0.002
Temperature	10.3 (28.8) %	12.73	0.002
Proportion of intensive land cover	24.5 (65.9) %	36.04	0.002
Mean soil pH	23.5 (64.3) %	34.16	0.002

Table 3: Results from Redundancy Analysis (RDA) analyses. The unconstrained first Principal components Analysis (PCA) axis explained 35.4% of the total variation in the multivariate dataset. Rows below show the proportion of this total variation explained by each constraining variable. The figures in brackets indicate the proportion of the variance in the unconstrained first axis explained by each variable (i.e. rainfall explains 35.2% of 35.4%)