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Error propagation associated with benefits transfer-based mapping of ecosystem services

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ABSTRACT

An increasing number of studies are taking the important first step in global efforts to conserve key ecosystem services by mapping their spatial distributions. However, a lack of primary data for most services in most places has largely forced such mapping exercises to be based on proxies. The common way of producing these proxies is through benefits transfer-based mapping, in which estimates of the values of services are obtained from a small region for particular land cover types, and then extrapolated to a larger area for these same types. However, the errors that may result from such extrapolations are poorly understood. Here, we separate the generalization errors associated with benefits transfer mapping into three constituent components – uniformity, sampling, and regionalization error – and evaluate their effects using primary data for four ecosystem services in England. Variation in ecosystem services within a particular land cover type (uniformity error) alone led to a poor fit to primary data for most services; sampling effects (sampling error) and extrapolating from a small region to a larger area (regionalization error) led to substantial, but highly variable, additional reductions in the fit to primary data. We also show that combining multiple ecosystem services into a single layer is likely to be even more problematic as it contains the errors in each of the constituent layers. These errors are sufficiently large to undermine decisions that might be based on such extrapolated maps. Greatly improved mapping of the actual distributions of ecosystem services is therefore needed to achieve the goal of conserving these vital assets.

1. Introduction

There has been a rapid increase in the number of studies mapping the spatial distribution of ecosystem services since the Millennium Ecosystem Assessment (2005) heightened awareness of the importance of such services for human well-being. These maps are vital because the development of strategies for maintaining key ecosystem services begins with determining where they are provided (Naidoo et al., 2008). Recent mapping studies include global (e.g. Turner et al., 2007; Naidoo et al., 2008; Luck et al., 2009), country-wide (e.g. Egoh et al., 2008; Ingraham and Foster, 2008; Anderson et al., 2009; Eigenbrod et al., 2009), and regional assessments (e.g. Naidoo and Ricketts, 2006; Troy and Wilson, 2006; Raymond et al., 2009).

Due to a lack of primary data in most places (cf. Naidoo et al., 2008), maps of the distributions of ecosystem services have principally been based on proxies. The most common way of producing these proxies is using benefits transfer (Plummer, 2009) – also known as spatial value transfer (Troy and Wilson, 2006) – recent applications of which have involved taking estimates from a small region and assuming these can be applied over a larger area (e.g. Eade and Moran, 1996; Sutton and Costanza, 2002; Metzger et al., 2006; Troy and Wilson, 2006; Turner et al., 2007; Petrosillo et al., 2009). For example, to estimate the spatial distribution of the values of ecosystem services in Massachusetts, Troy and Wilson (2006) collated estimates from 65 studies, most of which

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were measured outside the state. They used these to estimate the average ecosystem service values for each of nine land cover types, and then mapped the distribution of services across the whole state by assuming that the values of ecosystem services were constant within each land cover type. However, clearly values of ecosystem services are likely to vary considerably within a land cover type (Plummer, 2009). For example, the forests and agricultural buffers of the Catskill and Delaware Mountains of New York State have been valued at USD 6 billion (in avoided construction costs for water treatment plants) for water filtration (National Research Council, 2000), but similar forests and agricultural lands in locations with lower downstream population densities will have much lower ecosystem service values. Consequently, ecosystem service mapping based on benefits transfer may result in considerable error; the implications of such error for conclusions from these exercises remain poorly understood.

Plummer (2009) identifies 'generalization error' as being the key source of potential error in benefits transfer mapping. Generalization error can be subdivided into three main components:

1. *Uniformity error: a* major assumption in recent applications of benefits transfer-based mapping is that the value of an ecosystem service is constant (uniform) for a particular land cover type. For example, this logic assumes that biodiversity value is the same for all woodland regardless of its composition and management history, or that agricultural productivity is the same for all croplands. Uniformity error is therefore likely to be a major problem because ecosystems are very unlikely to have constant biophysical characteristics and the ecosystem services they provide will not be constant within a land cover type. Indeed, in earlier work, we show that uniformity error alone makes ecosystem service maps created through benefits transfer unsuitable for identifying hotspots or priority areas for multiple services (Eigenbrod et al., 2010).
2. *Sampling error*: the potential magnitude of sampling error above and beyond uniformity error is also considerable. This is because the choice of 'study sites' (Rosenberger and Stanley, 2006) for estimating values of an ecosystem service is usually very limited. At best, several studies are available (but often only one) in which the value (economic or otherwise) of an ecosystem service has been quantified for a particular land cover type. Having a small number of available measurements increases the risk of sampling artefacts being introduced into value estimates, even if the samples are otherwise representative.
3. *Regionalization error: in* addition to being few in number, study sites have typically been small and geographically localised in recent applications of benefits transfer, relative to the area being mapped, and so they may not be representative of the region as a whole. For example, in a recent assessment of the ecosystem service value of the United States National Wildlife Refuge system, the value of freshwater regulation and supply was based on a single study from California for wetlands, and another study from Minnesota for open water (Ingraham and Foster, 2008). Likewise, in the seminal study of Costanza et al. (1997) and its successors (e.g. Sutton and Costanza, 2002; Turner et al., 2007; Petrosillo et al., 2009), a single study from Veranasi, India (Mishra, 1969) was used to assign the nutrient cycling value for all tropical forests globally. Generalising from a localised well-studied area to a wider region may introduce particular extrapolation problems – hereafter 'regionalization error' – because relationships among ecosystem services have been shown to demonstrate geographic variation (Anderson et al., 2009).

Our goal in this study is to evaluate the effects of these three components of generalization error – uniformity, sampling and regionalization error – on benefits transfer-based mapping of ecosystem services in a clearly defined case study for four ecosystem services in England. Our study is the first to dissect the effects of the different components of generalization error, and builds on earlier work quantifying the effect that uniformity error alone has on benefits transfer-based mapping of ecosystem services (Eigenbrod et al., 2010). In the existing literature, sampling and regionalization errors usually go hand in hand because one or a few studies are usually localised in their distribution; we are able to examine these two types of errors independently. This work has important implications for conserving ecosystem services, as a vital first step to reducing errors in benefits transfer mapping is to dissect the effects that different components of such error have on analyses. Note that we focus on the impact of the biophysical component of generalization error here, and not on the impact of variation in the economic values between study sites and the area being mapped, but the same sources of uncertainty would often apply to spatial variation in economic estimates of value as well.

2. Methods

2.1. Creation of ecosystem service maps

To quantify the effects of the three components of generalization error on ecosystem service mapping, we compared the accuracy of maps created through benefits transfer (proxies) with maps from the same area based on primary data. We focus on biophysical variation in four ecosystem services across England, quantifying each service in units per area (in this case per 2×2 km grid square) that describe it most effectively. We used England-wide primary data surfaces for four ecosystem services (Anderson et al., 2009; Eigenbrod et al., 2009). These were: (a) a distribution map of biodiversity of taxa of conservation concern (UK Biodiversity Action Plan (BAP) species from several taxonomic groups; (Anon., 1994); (b) nationwide representative sampling data from 2711 points of rural recreation use (Natural England, 2006); (c) a surface of carbon storage based on extensive field data; and (d) a surface of the value of agricultural production (gross margin = value of output − variable costs, with subsidy payments removed), based on agricultural census data. We used monetary values for the agriculture layer as this allowed us to combine the disparate types of agricultural output and map the biophysical variation in agricultural production in England as a single surface. Biodiversity as a whole is thought to be instrumental in supporting all ecosystem services (e.g. Balvanera et al., 2006), and is therefore often not held to be an ecosystem service in itself. However, we consider biodiversity of taxa of conservation concern to be an ecosystem service per se through its existence value; indeed their value to British society is reflected by their prioritization for conservation through government policy (the Biodiversity Action Plan). The link between biodiversity and ecosystem processes, while clearly very important, is not the focus of this study and is not therefore discussed further.

Detailed methods for the creation of these primary data surfaces are available in the Supplementary materials.

We used data from our primary data surfaces to assign values to fourteen land cover classes (mapped at 2×2 km grid resolution; Supplementary materials) to construct ecosystem surface maps based on benefits transfer. Our approach differs from many studies in that we use estimates solely taken from within the study region, rather than relying on estimates collected from outside the study region altogether (cf. Troy and Wilson, 2006). We tested the relative importance of the three components of generalization error by altering both the number and locations

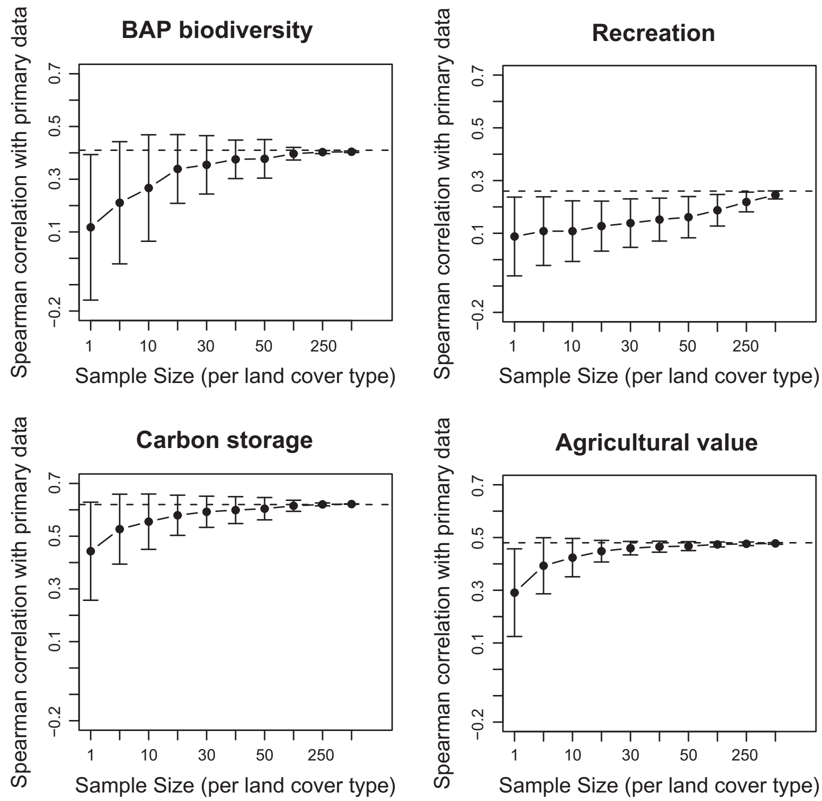

Fig. 1. The effects of uniformity and sampling error on correlations between land cover based proxies and primary data for four ecosystem services. The heading "BAP biodiversity" refers to biodiversity of taxa of conservation concern (UK Biodiversity Action Plan species). The effects of the sample size (number of 2×2 km^2) used to calculate the value of an ecosystem service for each of eight land cover types on the Spearman correlation (mean from 1000 runs ±1 SD) between primary data and the land cover based proxy are shown by the ♦ on the solid lines. For some land cover types, the total number of 2×2 km grid squares is as few as 27 for all of England. For such rare land cover types, if the total number of grid squares is less than the sample size, the maximum sample size possible is used (all possible grid squares). Consequently, the larger samples (100+) are only samples of the most common land cover types (cropland, pastureland, urban areas). The Spearman correlation between primary data and the land cover based proxy based on all primary data (uniformity error; n = 10,939) is shown by the dotted horizontal lines.

Table 1
The impact of regional vs. random sampling on the correlation (mean from 1000 runs ±1 SD) of land cover based proxy maps with maps based on primary data at the 10×10 km grid resolution. For regional sampling, the ecosystem service value of each land cover type was based on all primary data values for this land cover type within a single randomly selected 100×100 km^2; for the random sampling, the estimate was based on the same number of primary data values as in a given randomly selected 100×100 km^2 for a land cover type, but selected randomly across all of England. The mean correlations are based on 1000 runs, calculated across all land cover types for each run. The average number of 2×2 km grid squares per land cover type within a 100×100 km^2 is 19 ± 5 SD.

Ecosystem service	Regional sampling	Random sampling – same sample size	Random sampling – single sample
Type of generalization error	Uniformity error + regionalization error	Uniformity error	Uniformity error + sampling error
Biodiversity of taxa of conservation concern	0.05 ± 0.28	0.32 ± 0.14	0.12 ± 0.28
Recreation	0.12 ± 0.11	0.14 ± 0.12	0.09 ± 0.15
Carbon storage	0.52 ± 0.14	0.59 ± 0.07	0.44 ± 0.19
Agricultural production	0.30 ± 0.17	0.45 ± 0.06	0.29 ± 0.17

of the 2×2 km grid cells from the primary data surfaces that we used to obtain values for each of the land cover types (Fig. 1 and Table 1).

First, to test the effect of uniformity error, we used the average of all primary data values for England that coincided with a particular land cover type (cf. Eigenbrod et al., 2010) to assign a single (average) value for each ecosystem service to each land cover type. These fixed values were combined with the geographic distribution of each land cover type to produce maps of the distributions of all four ecosystem services. Any lack of concordance between these proxy (benefits transfer based) surfaces and the primary data surfaces is thus entirely due to variance within habitat type in the primary data caused by uniformity error (sample error is controlled because the entire data set is used to derive the averages; regionalization error is controlled because the data for all regions are included). Detailed methods for the creation of the proxy maps are available in Supplementary materials.

Second, we constructed a set of proxy surfaces to quantify the effect of sampling error. In these, we randomly selected a sample of the total number of primary data values for each land cover type, and used the average from this sample to estimate the value of an ecosystem service for the land cover type. We then increased the sample size and repeated the procedure. This approach examines error introduced when values for an ecosystem service for a land cover type are based on only a few or even one study, as has often been the case in recent applications of benefits transfer. For this set of surfaces, lack of concordance with the primary data is due both to uniformity error and sampling error. Note that both sampling error and uniformity error are being driven by variation in the biophysical value of ecosystem services within a land cover type, so as sample size increases, the effects of sampling error decreases until, at the limit (when sample size equals the total number of primary data values (the population) for all land cover types), only uniformity error remains.

Finally, we constructed a third set of proxy surfaces to quantify the effect of regionalization error. In Anderson et al. (2009), we demonstrated considerable regional variation in relationships among ecosystem services across 100×100 km grid squares in England. We use the same areas to examine the effects of regionalization on benefits transfer estimates. We used the average value of all primary data values from a randomly selected region of England (100×100 km grid square) (Fig. S1) for each land cover type to estimate the value of an ecosystem service for the land cover type for all of England. To control for the sampling error in this analysis (the average number of 2×2 km cells per land cover type for each region was 19 ± 5 SD), we also selected a random sample of all primary data values in all of England where the sample size was the same as in the randomly selected 100×100 km^2 for each land cover type. This 'pairing' of each randomly selected region with an equal number of 2×2 km^2 selected from all of England allowed us to examine the effects of regionalization error independently of sampling error.

2.2. Analyses

We ran two sets of analyses to quantify the impact that the three components of generalization error can have on inferences drawn from ecosystem service mapping studies based on benefits transfer. First, we calculated the Spearman rank correlation between the primary data and proxy surfaces based on either: (a) the average values of all primary data for each land cover type (the effect of uniformity error alone); (b) the average value of one to 1000 randomly selected 2×2 km primary data squares (the effect of uniformity error + sampling error) for each land cover type (Fig. 1); and (c) the average value of all 2×2 km primary data squares for each land cover type in a randomly selected 100×100 km region (Table 1). We based the Spearman correlations on 10×10 km maps for all services based both on primary and proxy data, as the relatively sparse sampling of the recreation layer meant that comparisons between the proxy and primary data layer for this service were not meaningful at the 2×2 km resolution. We created these 10×10 km maps for the individual layers by calculating the mean value of all 2×2 km grid squares within a 10×10 km^2 for both the proxy and primary data surfaces for each service. Note that since ecosystem service values vary within 10×10 km grid squares, our results tend to underestimate the true errors associated with the different elements of generalization error, making our conclusions conservative.

Second, we looked at the effect that uniformity and sampling error would have on attempts to identify areas that are most important for providing multiple ecosystem services; data limitations precluded us from including regionalization error in this second analysis. Prioritising areas for protection based on multiple services (Chan et al., 2006) or combining a suite of ecosystem services into a single value (e.g. Turner et al., 2007; Luck et al., 2009) are both increasingly common in the literature. We used a deliberately simple approach to combine ecosystem services, as our primary goal here was to quantify the effect of generalization error on our results and not actually to select the best areas in England for providing multiple services. We standardized the values of the four ecosystem services (biodiversity of taxa of conservation concern, agricultural production, recreation, and carbon storage) so they each ranged from 0 to 100. We then simply added up these standardized layers at the 10×10 km resolution, assuming equal weighting for all four layers. We then calculated the Spearman rank correlations between the ranking of sites found to be important for providing multiple ecosystem services based on primary data and the proxy surfaces (Fig. 2).

All GIS analyses were carried out in ArcGIS/ArcInfo 9.2 (ESRI, Redlands, California, USA). All statistical analyses and randomizations were carried out in R 2.7.2 (R Development Core Team, 2008). The R packages *sciplot*, *maptools*, and *pgirmess* were used for figure creation.

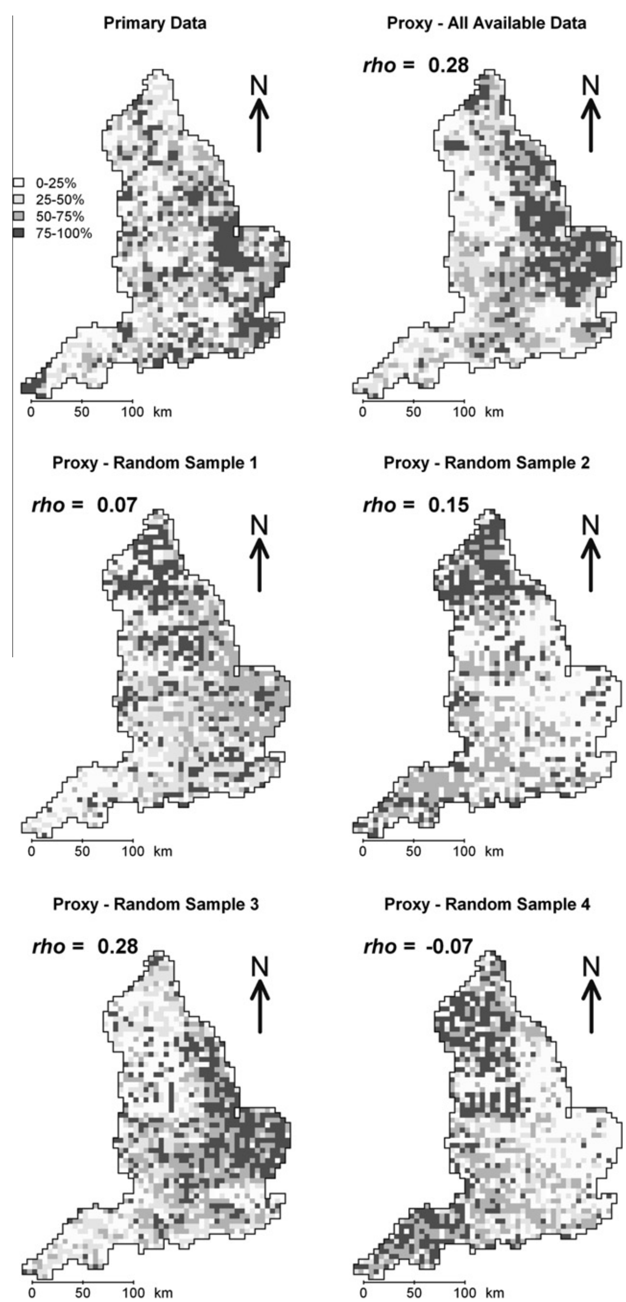

Fig. 2. Distribution of multiple ecosystem services (biodiversity of taxa of conservation concern, recreation, carbon storage, and agricultural production combined into a single layer) based on primary data, proxy data based on mean values from all primary data, and proxy data based on a single random sample of the primary data per land cover type ("random samples 1–4"). The random samples shown are four out of the 1000 runs we performed for this analysis. The correlations (Spearman's *rho*) between the primary data and the respective land cover based proxy data surfaces are also shown.

3. Results

Overall, uniformity error alone was sufficient to result in a very poor overall fit of the land cover proxy to the primary data for all four ecosystem services considered (horizontal lines in Fig. 1). Sampling error (Fig. 1) and regionalization error (Table 1) both led to further reductions in the fit to the primary data. There was, however, considerable variation between ecosystem services in the effects of these three components of generalization error.

Uniformity error alone was substantial for all services (Fig. 1). However, the rank correlation between the land cover proxy based on all data and the primary dataset was nearly three times as great for carbon storage (mean Spearman's *rho* = 0.62) as for recreation (*rho* = 0.26), with intermediate associations for agricultural production (*rho* = 0.48) and biodiversity of taxa of conservation concern (*rho* = 0.41).

Sampling error had the largest effect on biodiversity of taxa of conservation concern, resulting in further reductions in the correlation coefficient between the proxy and primary data from 0.41 to 0.12, when only a single sample was taken (Fig. 1). Reductions due to sampling error for the other three services were approximately 0.15. There was also a large increase in the fit of the proxy to the primary data for both carbon storage and agricultural production when going from a single sample to five samples, and fit of the proxy similar to that based on all available data when at least 20 samples were taken from each land cover type. There was a less marked increase in the fit of the proxy to the primary data for biodiversity of taxa of conservation concern when going from one to five samples, and the fit to the proxy was similar to using all data only after 30 samples were used. By contrast, there was no increase in the fit for recreation until at least 100 samples are used, and even using 250 samples gives a noticeably worse fit than using all available data (Fig. 1).

Including regionalization error also reduced the strength of correlations, relative to uniformity error alone, but the extent to which this occurred depended on the ecosystem service considered (Table 1). For biodiversity of taxa of conservation concern, extrapolated surfaces based on data from single 100×100 km regions were virtually uncorrelated with the primary data for the country as a whole, and were even worse than selecting just a single random sample per land cover type. However, regionalization error was small for recreation and carbon storage within England. For these two ecosystem services, surfaces based on regionalization error plus uniformity error performed nearly as well as surfaces based on uniformity error alone (Table 1).

Uniformity error also had a major effect on the degree of correlation between the priority ranking of sites important for multiple ecosystem services (biodiversity of taxa of conservation concern, recreation, carbon storage and agricultural production) based on primary data vs. the proxy data (Fig. 2). The Spearman rank correlation for uniformity error alone was 0.28, indicating that the uniformity error for the combined ecosystem services surface was greater than for three of the four individual ecosystem services (Fig. 1). A single randomly selected sample of the primary data, thus incorporating sampling error as well as uniformity error, generated even lower correlations with the raw data, averaging 0.07 ± 0.19, based on 1000 sampling runs. As suggested by the confidence limit, and illustrated by the four randomly drawn samples (Fig. 2), surfaces derived from different single samples lead to very different spatial prioritisations of the landscape.

4. Discussion

This study is the first to dissect the three major components of generalization error in benefits transfer estimates when considering spatial variation in ecosystem services, and to consider the effects of this error on attempts to prioritise sites based on levels of ecosystem service provision. We show that variation in ecosystem services within a particular land cover type (uniformity error) is sufficient to result in a poor fit of the land cover proxies to the primary data, but that sampling effects (sampling error) and extrapolating from a small region to a larger area (regionalization error) also lead to substantial, but highly variable, additional reductions in the fit of the proxies to primary data. We also show that combining ecosystem services into a single layer (sensu Turner et al., 2007; Luck et al., 2009) is likely to result in similarly high or even greater levels of generalization error, again primarily through uniformity error but with a substantial and variable contribution of sampling error (regionalization error was not considered for multi-service surfaces).

Uniformity error alone led to a poor fit of the land cover based proxies created through benefits transfer mapping for all ecosystem services in this study, with correlations less than 0.6 in all cases, even using ranked data. It is likely that such high variation in ecosystem services within a land cover type will generally be very common (Plummer, 2009). For example, Hörnsten and Fredman (2000) show that the value of forests in Sweden for recreation decreases with distance from residential areas, so it is not surprising that assigning a spatially uniform value to recreation for forests (as was also done by Metzger et al. (2006) and Turner et al. (2007)) resulted in considerable error. Or, in another example, Boyd and Wainger (2002) show that the drinking water benefits of wetlands selected as a 'mitigation bank' for other wetlands lost through development in Florida were lower due to factors such as the proximity of beneficiaries and future threats from invasive species. Our results also indicate that uniformity error will be considerable even for 'global' services (Hein et al., 2006) such as carbon storage or sequestration. A possible solution to improving the fit of benefits transfer based proxy data to primary data for services whose values are dependent on their spatial context is to weight the proxy surfaces by the key drivers of these relationships (e.g. Chan et al. (2006) for recreation, flood control, and pollination). In earlier work, we showed that such an approach was somewhat effective for improving proxy surfaces for recreation (Eigenbrod et al., 2010). However, this effectiveness will depend on how well the variables determining the regional values of a service are understood, and such knowledge is likely to be poor for the services for which benefits transfer mapping is most often used.

The degree of spatial autocorrelation (Tobler, 1970) in the ecosystem services considered here offers the most parsimonious explanations for the observed variation in sampling error and regionalization error between services. Post-hoc Mantel's tests showed that spatial autocorrelation is high (Moran's $I \sim 0.20$) for biodiversity of taxa of conservation concern for distances over 100 km, and high (Moran's $I > 0.20$) for carbon storage and agricultural production for distances of 50 km, but generally very low (Moran's $I < 0.05$) for recreation (Fig. S2). The presence of substantial spatial autocorrelation in all services except recreation likely explains why relatively limited sampling (20–30 2×2 km^2 randomly selected from across the country) was nearly as good as using the country-wide average for carbon storage, agricultural production and biodiversity of taxa of conservation concern, but not for recreation. Strong regional variation in ecosystem services has already been shown to lead to diametrically opposing conclusions about correlations between ecosystem services (Anderson et al., 2009); our results here indicate the dangers in ecosystem service studies of extrapolating results from particularly well-studied regions to wider landscapes that contain them.

In theory, careful consideration of the scale of the key biophysical and economic determinants of ecosystem services could inform future mapping exercises by giving investigators some a priori idea of the spatial patterns of the services being considered. For example, spatial autocorrelation at distances of over 100 km for biodiversity of taxa of conservation concern in Britain is not surprising given that relatively broad-scale biophysical processes such as energy availability are known to affect patterns of species richness (e.g. Evans and Gaston, 2005) above and beyond differences due to different land cover types. Additional spatial differentiation may occur if economic values (e.g. non-use values based on contingent valuation surveys or choice experiments) are assigned to biodiversity due to regional (or even local) differences in people's interests in particular species, and differences in the socioeconomic makeup and size of human populations (Akter and Grafton, in press). By contrast, spatial autocorrelations are shorter for stored carbon in Britain, probably because soil carbon is partly determined by large-scale patterns of temperature and precipitation, and partly by more local variation in drainage, geology, soil type and land use. Land use can be thought of as both a consequence of ecosystem carbon (only a subset of land uses are feasible on water-saturated, carbon-rich soils) and a determinant of ecosystem carbon levels (e.g. through disturbance, drainage and harvesting); leading to stronger correlations between the land cover based proxy and the primary data for stored carbon than for biodiversity of taxa of conservation concern in this study. In addition, there will be little regional variation in the economic value of stored carbon, or, for that matter, agricultural production, due to the global nature of carbon and most agricultural markets. The relative and absolute extent of spatial patterns in ecosystem services will clearly be dependent on both the services and the geographic extent being considered (for example, globally spatial autocorrelation of stored carbon may well be greater than for biodiversity); the point we make here is that consideration of the scale of the biophysical processes driving such patterns could inform future mapping exercises by identifying the sampling intensity needed for benefits transfer-based mapping to provide reasonable estimates of ecosystem services. However, as discussed earlier, knowledge of what biophysical factors are driving many ecosystem services is often likely to be lacking, and even if known, detailed maps of the distributions of such biophysical drivers may not be easy to come by.

More generally, if the spatial scale of heterogeneity of the ecosystem services is well understood, this information can then be used to split land cover types into suitably sized regions. Such an approach can in principle reduce generalization error. For example, when looking at recreational use on beaches, Troy and Wilson (2006) use separate study sites to identify the value of beaches near dwellings to those away from dwellings. However, lacking better data on ecosystem services from the study region, it is hard to see how to discern the degree of disaggregation required to obtain improved estimates; such data limitations mean that the scope for such methods appears limited.

The extent of the impact of generalization error we show in this study makes it clear that more work needs to done to quantify the extent of the error in studies mapping ecosystem services. Studies such as ours, in which high-resolution data are degraded to explore the consequences faced in data-poor situations, should be repeated in places that are not densely populated temperate islands such as Britain, and even more importantly, repeated for services which we did not examine here. Indeed, many key ecosystem services have only been mapped over large regions based on benefits transfer or other land cover based proxies (e.g. pollination, pest regulation, soil accumulation, water purification, flood prevention) – more primary data for such services would have the benefit of allowing both better mapping of these services, and also increase understanding of the degree of error associated with proxy-based maps for these services. The conservation biology literature offers a variety of proven approaches to exploring the impacts of data limitations on studies mapping the distribution of biodiversity (e.g. Hurlbert and Jetz, 2007; Gaston and Fuller, 2009); such studies would be well-suited to forming the basis of a conceptual framework for further work examining the effects of errors in studies mapping ecosystem services.

Another issue that needs further work is the effects on ecosystem service mapping studies of the way that a particular service is defined or assessed. Once again, biodiversity is a good example. In this study, we define biodiversity as consisting of taxa of conservation concern, partly as these have policy relevance but also due to the limitations of England-wide datasets. However, it is likely that the economic value of biodiversity will be dominated by: (a) charismatic species (e.g. White et al., 2001) and/or (b) a few, likely common (Gaston, 2010), or even invasive (McCauley, 2006) species that are either of direct economic value or provide key ecosystem services; it is therefore very likely that patterns of the economic value of biodiversity will be very different to patterns of biodiversity based on the richness of all species or of species of conservation concern. An added concern is that if different methods are used to assess an ecosystem service in different regions and then combined – as has been done, for example, in most ecosystem service mapping exercises based on Costanza et al. (1997) – this could lead to considerable additional error.

However, while the extent of generalization error will vary between ecosystem services and regions, there is no a priori reason to believe that the magnitude of the errors observed here are unrepresentative. Indeed, it is very likely that our study provides an underestimate of the full extent of generalization error as our primary data surfaces, though based on primary data, are necessarily still homogenized 'smoothed' surfaces. In addition, spatial variation in economic valuations of ecosystem services and temporal variation in ecosystem services could add further error to maps based on benefits transfer.

In conclusion, we show that generalization error is a major source of error in benefits transfer-based mapping as it is currently conducted in the ecosystem services literature. In this case study, uniformity error was the major source of error, but sampling error and regionalization were often sufficient to remove what association remained between the proxy surface and with primary data after uniformity error was accounted for. We therefore suggest that benefits transfer mapping is only suitable for a very limited range of studies. It will be suitable when the heterogeneity of ecosystem services within a land cover type is low, as this will mean that uniformity error will be minimal; this situation might (for example) occur if only very small areas are being mapped and the underlying environmental variation in the region is small. Benefits transfer mapping can also be an adequate (and cost-effective) methodology if the goal of a study is simply to rank (and map) the relative importance of a small number of highly distinct land cover types in terms of their importance for one or more ecosystem services (e.g. carbon storage in peat bogs vs. fertilised grassland vs. cereal fields). However, even such qualitative ranking studies are only suitable where *all* ecosystem services have large differences in their values for *all* land cover types; again, such information is generally lacking. Our study suggests that this condition is unlikely to be met in landscapes containing a variety of land cover types. Improved mapping of the actual distribution of ecosystem services is therefore needed to provide the accurate estimates of the detailed distributions of ecosystem services that will be needed if global efforts to conserve these vital assets are to be successful.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.06.015.

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