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Full Length Article

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ABSTRACT

The ecosystem service literature has drastically expanded since the Millennium Ecosystem Assessment, yet the nature of how ecosystem services interact across space is still poorly understood. A key unresolved question is how efforts in sampling (a proxy for data availability) affect the calculation of the interactions or associations among ecosystem services. We contribute to answering this question by estimating a suite of ecosystem services and asking how the values of their interactions – in the form of spatial correlations – change as a function of the sampling rate of the landscape. Specifically, we estimate a set of seven ecosystem services for France (agricultural production potential, biodiversity, carbon storage, livestock grazing potential, net ecosystem productivity, pollination, and soil loss), applying four different measures for biodiversity, seven different methods for carbon storage, and three for pollination. We find that spatial correlations are fairly robust to the sampling rate, supporting the notion that moderate sampling rates across a heterogenous landscape are sufficient to obtain reliable estimates of the average correlation occurring across the landscape. In other words, despite heterogeneity in the spatial distribution of ecosystem services, at sufficient sample sizes we only need to randomly sample ten percent of the landscape to acquire an accurate measure of the correlations between all ecosystem services averaged across the entire landscape. Our results have implications for management, with applications for sampling extent and intensity and the identification of ecosystem service bundles.

1. Introduction

The ecosystem service literature has seen an explosion of publications since the Millennium Ecosystem Assessment (Bennett et al., 2009; Fisher et al., 2009; Vihervaara et al., 2010). Yet despite an immense number of case studies being published, the nature of how ecosystem services interact across space is still poorly understood (Bennett et al., 2009; Seppelt et al., 2011). Indeed, effective estimation of the spatial correlations among ecosystem services enables a better identification of ecosystem service bundles, which is key to managing the landscape so as to maximize total benefits.

The literature has progressed such that most papers measure at least a set of services and report the spatial correlations between them (Seppelt et al., 2011; Vihervaara et al., 2010), with a large variety of tools available to measure the provisioning or supply of ecosystem services (Crossman et al., 2013; Egoh et al., 2008; Martínez-Harms and Balvanera, 2012; Schagner et al., 2013). However, issues of data availability, quality, quantity, and uncertainty remain key limitations to the field (Crossman et al., 2013; Egoh et al., 2012; Hou et al., 2013; Layke et al., 2012; Martínez-Harms and Balvanera, 2012), and may largely impact the estimation of spatial correlations. A key unresolved question is how the effort in sampling (a proxy for data availability) affects spatial correlations – often referred to as interactions or associations, sensu Vallet et al. (2018) – among ecosystem services. On-the-ground estimates of ecosystem services are time consuming and expensive to conduct. Furthermore, even with proxy-based methods that rely on land use and land cover data, finding the balance between how much of the landscape is needed to accurately measure a spatial interaction is tricky. Sampling too much of the landscape can be expensive in terms of time, labor, computation time, and other costs; sampling too little can ignore local heterogeneities that are averaged out when calculating the spatial correlation.

We contribute to answering this question by estimating a suite of ecosystem services and asking how the values of their spatial

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correlations change as a function of the sampling rate of the landscape. Specifically, we estimate a set of seven ecosystem services for France (agricultural production potential, biodiversity, carbon storage, livestock grazing potential, net ecosystem productivity, pollination potential, and soil erosion prevention), applying four different measures for biodiversity, three for pollination, and seven different methods for carbon storage. We vary the sampling rate of the data to calculate the spatial correlations between our ecosystem services. We find that correlations are fairly robust to the sampling rate, supporting the notion that at sufficient sample sizes moderate sampling rates across a heterogeneous landscape are sufficient to obtain reliable estimates of the average correlation calculated using data for the entire landscape.

Relatively few studies have explicitly evaluated uncertainty in estimating ecosystem services. Plummer (2009) and Rosenberger and Stanley (2006) focus on the extrapolation and transferability of ecosystem service provisioning models, discussing the errors associated with taking the value of ecosystem services at one site and applying them to another. Eigenbrod et al. (2010) measure the overlap between on-site, local estimates of ecosystem services and proxy-based land use data. Schulp et al. (2014) reviewed and compared ecosystem service maps at the European scale. Van der Biest et al. (2015) test for differences in the spatial correlations between ecosystem services across three types of land use-based models and field data. Roussel et al. (2017) compare the clustering or bundling of ecosystem services between a proxy-based land use method and a set of models which compute seven other individual ecosystem services. Vallet et al. (2018) compared different methods to estimate the interactions between ecosystem services, including how they might change over time. Rather than comparing different models or data sources to measure ecosystem services at a single scale, we test for differences in the spatial correlations between ecosystem services as a function of the study sampling rate, while testing for differences between models and/or data sources for biodiversity, carbon storage, and pollination.

Our paper is outlined as follows: in the next section we present our framework for modelling ecosystem service provisioning, the data, and how we measure their interactions; our results are presented in the third section; finally, we discuss the main take-aways of our results and how they relate to ecosystem service management.

2. Methods

We model ecosystem services and their spatial interactions at the national scale of France. Data availability was and still is one of the major limitations of the field (Bennett et al., 2009; Crossman et al., 2013; Egoh et al., 2012; Hou et al., 2013; Layke et al., 2012; Martínez-Harms and Balvanera, 2012). Our study is no exception. We do not have access to local, plot-level data with which to test our hypotheses. We do, however, have access to national-level spatial data. As we will show below, for some of our results, the data can be viewed as a generic landscape – we would expect many of the general trends in our results to hold regardless of the spatial scale of the study. However, for other results such as policy implications, it will be more important to keep in mind that our study was conducted at the national level.

In terms of measuring the provisioning of ecosystem services, the literature is abound with different methodologies and modelling frameworks such as the InVEST model (Daily et al., 2009; Nelson et al., 2009), GUMBO (Boumans et al., 2002) and IMAGE (Schulp et al., 2012) frameworks, or the Soil Water Assessment Tool (SWAT) (Arnold et al., 1999; Lautenbach et al., 2013). We would direct the reader to reviews by Crossman et al. (2013), Egoh et al. (2012), Martínez-Harms and Balvanera (2012), and Schagner et al. (2013) for detailed discussions of the vast array of indices for measuring individual ecosystem services. We provide a summary spreadsheet in Supplemental Material A. Rather than taking one of the large modelling frameworks to estimate ecosystem service provisioning, we have chosen to take them as inspiration and build our phenomenological models of provisioning ourselves

directly from the literature. We believe that doing so increases the transparency of our work.

Furthermore, we modeled a set of seven ecosystem services, with four types of measurements for biodiversity, three for pollination, and seven for carbon storage, totaling eighteen indicators. While many case studies measure a larger number of ecosystem services, we find that considering a smaller set allows us to go deeper into understanding the data, the models, and how their interactions affect the calculation of the spatial correlation coefficients between ecosystem services, while balancing the limitations of data availability and quality for a study at the national scale. A summary of all ecosystem services and the methods used to measure them is found in Table 1.

We measured the spatial correlation coefficients between ecosystem services as a function of the percentage of the landscape sampled. Spatial correlation coefficients are often used synonymously with the terms "interactions" or "associations", though there is a body of work discussing what is an interaction versus an association, what are the types of interactions (tradeoffs and synergies), how do they form (directly or indirectly), and how do we measure them (see Lee and Lautenbach (2016) and Vallet et al. (2018) for overviews of this literature). Rather than be caught up in discrepancies about what-is-what, we will call our "interactions" for what they are: spatial correlations between ecosystem services across a given area.

Table 1
Summary of ecosystem service provisioning models.

Ecosystem service	Model description
Agriculture	Binary if annual summer or winter crops, orchards, or vineyards[a]
Biodiversity	
National Inventory of National Heritage	Number of threatened species of amphibians, birds, and reptiles[b]
Mauri et al. (2017)	Tree species richness[c]
Carbon storage (C)	
Amoatey et al. (2018) – Institutions	Power law relationship, C = 4735 * exp (0.7075 * NDVI)[d]
Amoatey et al. (2018) – Parks and gardens	Power law relationship, C = 3453.6 * exp (5.9194 * NDVI)[d]
Myeong et al. (2006)	Power law relationship, C = 107.2 * exp (0.0194 * NDVI)[d]
Yao et al. (2014)	Power law relationship, C = 6445.014 * (NDVI^2.390)[d]
Egoh et al. (2008)	Low/intermediate/high potential by land use type[e]
Gibbs et al. (2007)	Lookup table by land use type[e]
Spawn et al. (2020)	Aboveground carbon storage map[d]
Net ecosystem productivity	
Maes et al. (2015)	Net ecosystem productivity map
Pastureland	Binary if natural or intensive grassland[a]
Pollination (P)	
Ricketts et al. (2008)	Exponential function of distance to natural forest, P = exp (-0.00053 * distance)[f]
Schulp et al. (2014)	Map of percentage of suitable pollinator habitat
Schulp et al. (2014)	Map of pollinator visitation probability
Soil loss by water erosion	
Panagos et al. (2020)	Mean annual soil loss map[g]

Calculated at the 1 km resolution.
[a] Taken from the CESBIO land use and land cover data (https://labo.obs-mip.fr/multitemp/) (10 m resolution).
[b] As listed by the National Inventory of Natural Heritage (INPN) (https://inpn.mnhn.fr/) (10 km resolution).
[c] Compiled from species occurrence data, aggregated using a 10 km grid (10 km resolution).
[d] Associated data from the Google Earth Engine are reported at < 1 m resolution.
[e] Corresponding values of carbon storage by land use type can be found in the Supplemental Material (10 m resolution).
[f] Natural forest data is provided by the European Commission Joint Research Centre forest cover data (https://forest.jrc.ec.europa.eu/en/) (25 m resolution).
[g] Estimated using the revised universal soil loss equation (RUSLE) (100 m resolution).

2.1. Measuring ecosystem service provisioning

As data availability and quality are key limitations, we relied primarily on land use and land cover data in our models to estimate ecosystem service provisioning, though there are notable exceptions as discussed below. Land use and land cover data were downloaded from the French Centre d'Etudes Spatiales de la Biosphère (CESBIO) (Inglada et al., 2017) at the 10 m resolution. It includes seventeen land use types: annual summer crops; annual winter crops; broad-leaved forest; coniferous forest; natural grasslands; woody moorlands; continuous urban fabric; discontinuous urban fabric; industrial and commercial units; roads; bare rock; beaches, dunes, and sand; water bodies; glaciers and perpetual snow; intensive grasslands; orchards; and vineyards. Additionally, we used biodiversity data compiled from the National Inventory of Natural Heritage (INPN) (10 km resolution), reflectance data taken from the Google Earth Engine (<1 m resolution), and forest cover as provided by the European Commission Joint Research Centre (25 m resolution). References for where to download spatial data are located in Table 1 and, if available for public download, can be accessed on the Open Science Framework (osf.io/7hk9v).

It is worth keeping in mind that in order to measure the correlations between ecosystem services, we must align their associated raster data layers, which requires that they be the same spatial extent and resolution. It is necessary to interpolate or aggregate (downscale or upscale) the data to be the same resolution. We aggregated to the resolution of the coarsest layer which, in doing so, transforms our binary measures of ecosystem services (e.g., agriculture and grazing) into continuous measures of potential probabilities of presence based on their proximity to cell(s) with a presence of the service.

2.1.1. Agriculture potential

As France possesses a large agricultural system across the country (about a third of the country's total surface area in 2018[1]) and a high degree of variation in its crops produced (exporting 346 different types of crop and livestock products in 2018[2]), we limited our study of agricultural production to a binary agriculture/not agriculture index. To be clear, agricultural data for France does exist. Aggregated data at the departmental level can be accessed online via the Service Statistique Ministériel de l'Agriculture (Agreste).[3] Parcel-level data of major agriculture types are available for each department through the Agence de Services et de Paiement (APS) and the Institut National de l'Information Géographique et Forestière (IGN).[4] Specifically, this data is part of the Registre Parcellaire Graphique (RPG), which is an annual declaration agricultural parcels and their corresponding surfaces in accordance with the acquisition of EU subsides from the Common Agricultural Policy. However, due to the large diversity of agricultural products in France, we believe that a proper treatment of this data is better left for future studies.[5] The presence or absence of agriculture was taken from the CESBIO land use and land cover data set. We defined a pixel of agriculture land to be annual summer or winter crops, orchards, or vineyards. We find that differentiating between agricultural types is more important when considering the economic value of the ecosystem service, where benefits and costs between crop types becomes more important.

2.1.2. Biodiversity

While biodiversity is not an ecosystem service *per se*, it is known to be positively correlated with regulating services such as carbon sequestration, pest regulation, and soil mineralization (Cardinale et al., 2012; Millennium Ecosystem Assessment, 2005). However, fine-scale national surveys of biodiversity are few and far between. For example, through the L'Inventaire National du Patrimoine Naturel or National Inventory of Natural Heritage (INPN), it is possible to construct maps of species richness by taxonomic groups – but this is at the departmental level. Therefore, we used taxonomic species richness of threatened or protected species, where we have data at the national level, as a measure for biodiversity. Data were compiled from the National Inventory of Natural Heritage (INPN).[6] The database is based on an atlas (grid) of 10 km spatial resolution, where species occurrences are aggregated by taxonomic groups to produce a series of biodiversity maps for protected species across the country. We focused on certain taxonomic groups with different environmental requirements, thus representing different facets of biodiversity. Namely, we produced maps for threatened amphibians, birds, and reptiles. Similar approaches have been applied in the United Kingdom using the Biodiversity Action Plan (BAP) list of species of "conservation concern" (Anderson et al., 2009; Eigenbrod et al., 2009; Eigenbrod et al., 2010), and numbers of threated or protected species are often used as proxies for biodiversity in economic valuation studies (Bartkowski et al., 2015).

However, biodiversity of threatened or protected species does not necessarily correlate with common ones. In other words, it may not be a good proxy for the biodiversity of common species, as the "number of threatened species" and "number of total species" can be driven by different processes. Threatened species may exist as endemic, refugia populations with specific distribution patterns or may be oversampled compared to common species (though the potential contribution of rare species as keystone species cannot be completely discounted). Therefore, we supplemented our maps of threatened species with a well-established map of tree biodiversity in Europe (Mauri et al., 2017). In its raw form, the data exist as occurrences of 242 species across the European Union, compiled from existing European tree distribution datasets (Forest Focus and Biosoil) and previously unpublished National Forest Inventories datasets. We overlaid the raw data onto a 10 km by 10 km grid and aggregated species occurrences by species type within each grid cell to measure tree species richness at the 10 km resolution.

2.1.3. Carbon storage potential

As carbon is one of the more well-studied ecosystem services in the literature (Crossman et al., 2013; Feld et al., 2009; Issa et al., 2020; Martínez-Harms and Balvanera, 2012; Seppelt et al., 2011), we adopted a set of models to estimate carbon storage potential and investigate the uncertainty around the choice of method. We first used two look-up table approaches based on land use type. The first assigns a categorical "low", "intermediate", or "high" carbon storage potential based on the type of land occupation (Egoh et al., 2008; Rouget et al., 2004). The second attaches a more quantitative weight to carbon storage potential, assigning an average quantity of carbon stored per hectare for each pixel of each land use type at a given moment in time (Bai et al., 2011; Chan et al., 2006; Maes et al., 2012; Naidoo et al., 2008; Spawn et al., 2020; Swetnam et al., 2011; Vallet et al., 2018). Specifically, we used the carbon storage values of Gibbs et al. (2007), which is based on the Intergovernmental Panel on Climate Change guidelines for national greenhouse gas emissions (Intergovernmental Panel on Climate Change, 2006). Tables for the values of carbon stored per hectare of land use type can be found in Supplemental Material B. We complemented this measure with the aboveground carbon storage map of Spawn et al. (2020), which is based on a suite of local, regional, and national data sets including national inventories. Each of these approaches were

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motivated by the literature and/or expert opinion and lend themselves well to large-scale analyses, but ignore spatial heterogeneities across landscapes with the same land use. Therefore, they should be seen as averages rather than absolute values.

In an effort to account for finer-scale variation across the landscape, we followed the methodology of Dong et al. (2003), Myeong et al. (2006), Yao et al. (2014), and Amoatey et al. (2018), who relate aboveground carbon storage and reflectance data, the latter measured by the normalized difference vegetation index or NDVI. Each fitted non-linear models (usually saturating functions such as power laws) of on-the-ground field measurements of carbon storage to spatial reflectance data. We obtained NDVI data from the Google Earth Engine (Ermida et al., 2020; Jiang et al., 2008)[7] and transformed values of NDVI to carbon storage per pixel using the functions derived by Myeong et al. (2006), Yao et al. (2014), and Amoatey et al. (2018). It is worth noting that their field experiments were based in arid climates (Amoatey et al., 2018) or urban centers (Myeong et al., 2006; Yao et al., 2014), and so it is unlikely that these functions will produce precise estimates of carbon storage for other ecosystems like forests. However, rather than viewing the transformed carbon storage data in absolute terms, we used these models to give us a representation of carbon storage potential, and, by measuring a suite of parameterizations, tested the sensitivity of carbon storage estimation to model parameters.

Ideally, we would want to include finer scale assessments of carbon storage such on-the-ground field surveys throughout the country (Gascoigne et al., 2010; Gleason et al., 2008) or compartmental or process-based models calibrated to field data (Crossman et al., 2011b; Landsberg and Waring, 1997; Naidoo and Ricketts, 2006; Naidoo et al., 2008; Schulp et al., 2012). However, obtaining the necessary fine scale data was not possible at the national scale.

2.1.4. Grazing potential

We considered pastureland or grazing as a binary pastureland/not pastureland variable. Like agriculture, accurately classifying pastureland by species and production type is difficult and compounded by the fact that farmers may routinely share their land between multiple flocks. These difficulties are more apparent when attaching a value to a parcel, which depends on the species and eventual use of the animal product(s) (cheese, fur, meat, milk). We set a pixel to be pastureland if it is classified as a natural or intensive grassland in the CESBIO land use and land cover data set.

2.1.5. Pollination potential

We adopted the methodology of Ricketts et al. (2004) and Ricketts et al. (2008), who through a series of field experiments established a relationship between pollinator visitation rates and distance to natural forest. We used the European Commission Joint Research Centre (JRC) Pan-European forest cover map to create a proximity map of the distances of the centers of each pixel to the nearest natural forest pixel (broad-leaved, coniferous, or mixed). We then fitted the proximity data to the function defined in Ricketts et al. (2008) to estimate the mean visitation probability for temperate regions. We supplemented our pollination map with two maps by Schulp et al. (2014), which include the percentage of suitable pollinator habitat and the probability of pollinator visitation. Both maps are based on Corine land cover and landscape green elements data.

2.1.6. Regulating ecosystem services: Soil loss and net ecosystem productivity

We supplemented our core analysis with published maps of two regulating ecosystem services: soil loss (erosion prevention) (Panagos et al., 2020; Panagos et al., 2015) and net ecosystem productivity (Maes

et al., 2015). The former is based on the universal soil loss equation (USLE) (Batjes, 1996; Nelson et al., 2009; Wishmeier and Smith, 1978), which relates soil properties, topology, land management and vegetation cover, and precipitation to predict potential soil loss by water erosion. Specifically, we used the published map of Panagos et al. (2020), who adopted the updated revised universal soil loss equation (RUSLE) to estimate mean annual soil loss rates (tons/hectare/year) across the European Union in 2016.

Net ecosystem productivity (NEP) is defined as an ecosystem's net accumulation of carbon, which depends on the balance between gross primary production and losses via plant and animal respiration, leaching, plant emissions, methane fluxes, and disturbances (Chapin et al., 2012). For ecosystems that experience little or no disturbances, then it is given primarily by the difference between carbon gains from plant primary production (photosynthesis) and carbon losses by respiration and leaching. We used the published net ecosystem productivity map of Maes et al. (2015), prepared as part of an European Commission Joint Research Council report to measure spatial–temporal trends in ecosystem services across the European Union. Specifically, they used reflectance data as a proxy for net ecosystem productivity, defining it as the difference between net primary productivity and decomposition rates of dead organic matter (taken to represent heterotrophic respiration). They adopted the "Phenolo" algorithm of Ivits et al. (2013) to convert spatial maps of NDVI data to plant primary productivity, adjust for decomposition of dead organic matter, and normalize net ecosystem productivity to a dimensionless scale of 0 to 1.

To ensure data comparability, we aligned raster layers to the same spatial extent and resolution. Layers were resampled using a bilinear nearest-neighbor aggregation up to the resolution of the coarsest layer (10 km resolution), and then all layers were cropped to the same spatial extent using the '*raster*' package R v.3.6.2. By aggregating our binary, presence/absence measures of ecosystem service provisioning (e.g., agriculture and grazing), we implicitly transformed them to be a probability of presence based on their distance to a cell where the service is present.

2.2. Calculation of spatial correlation coefficients

We calculated the spatial coefficients between ecosystem services across a suite of random sampling rates of the landscape. That is, we randomly selected a certain percentage of pixels in the landscape (without replacement), and calculated the Pearson spatial correlation coefficients between each pair of ecosystem services using that subset of the data. While other methods exist in the literature for measuring interactions between ecosystem services such as principle component analysis, production possibility frontiers, or regressions (Feld et al., 2009; Lee and Lautenbach, 2016; Vallet et al., 2018), correlation coefficients are widely used, accepted, and provide reasonable estimates of interactions (Chan et al., 2006; Raudsepp-Hearne et al., 2010; Vallet et al., 2018). We then resampled the data and recalculated the correlations for $N = 1000$ repetitions, and calculated the mean and standard deviations for each pair of services for that percentage of the landscape sampled. We tested a set of proportions ranging from (0,100] percent of the landscape. As we are able to resample the landscape N number of times, and standard errors depend on sample size, hypothesis tests for statistical significance or p-values are largely inappropriate.

Analyses were carried out in R 3.6.2 using the '*raster*' and '*sp*' packages. Scripts for our analysis and final raster layers can be downloaded on the Open Science Framework (osf.io/7hk9v).

3. Results

3.1. Estimates of ecosystem service provisioning

Our estimations for ecosystem services are presented in Figs. 1 and 2. Agriculture and pastureland are inversely related, which is expected

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[7] As reflectance changes seasonally and annually, we specifically use the annual average between 2010 and 2020 for our analysis.
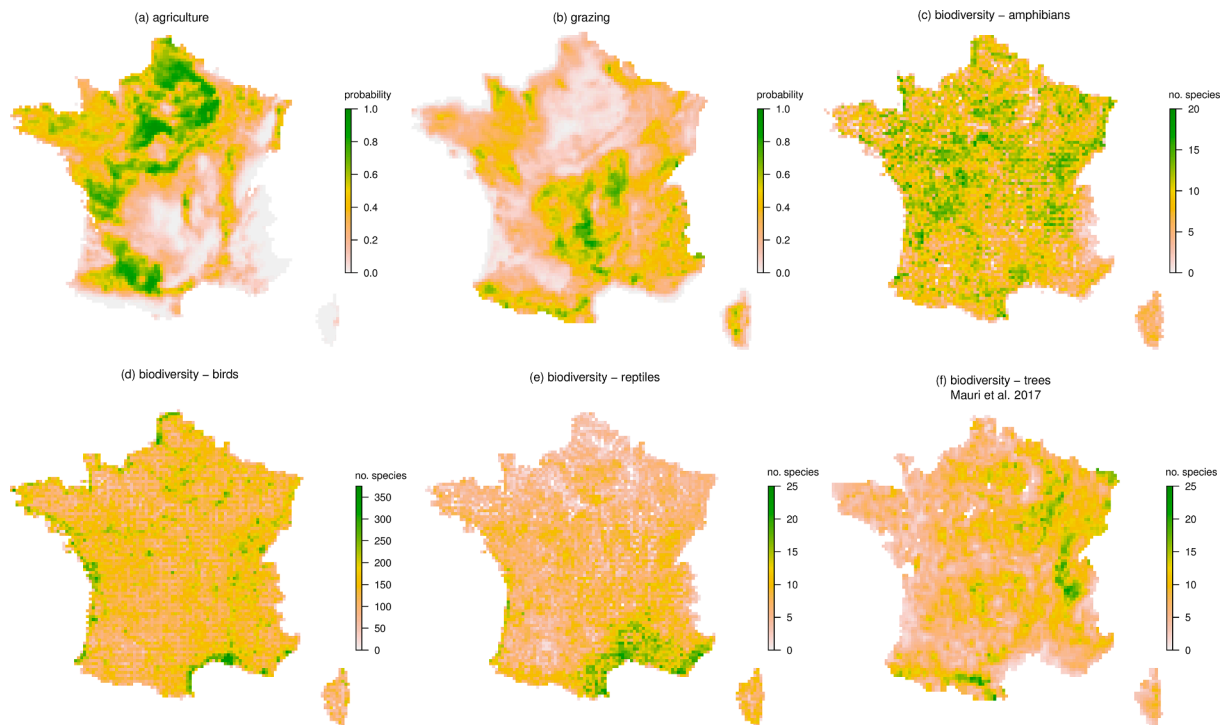
Fig. 1. Estimated ecosystem services: (a) agriculture; (b) pastureland; (c-e) biodiversity taken as the number of threatened or protected species amphibians, birds, and reptiles; (e) biodiversity measured as the number of tree species (Mauri et al., 2017). Note that the units in (a) and (b) are interpreted as the probability of the presence of agriculture and grazing.

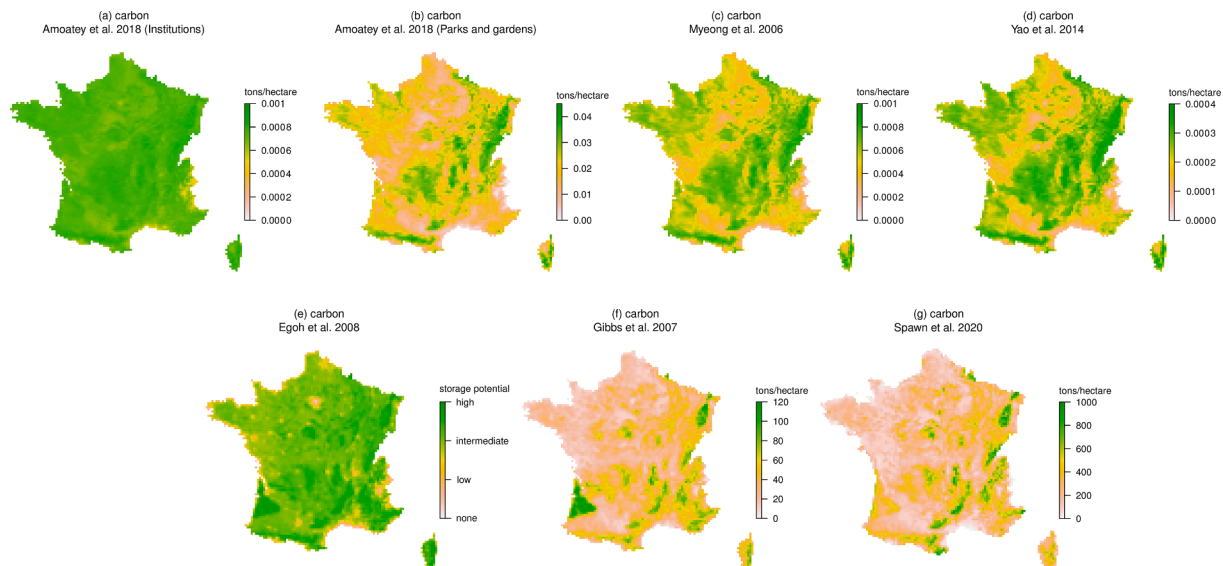**Fig. 2.** Estimated levels of carbon storage and carbon storage potential: (a) Amoatey et al. (2018) (institutions); (b) Amoatey et al. (2018) (parks and gardens); (c) Myeong et al. (2006); (d) Yao et al. (2014); (e) Egoh et al. (2008); (f) Gibbs et al. (2007); and (g) Spawn et al. (2020). Units for each measure are in tons/hectare.

given the modeling framework (Fig. 1a, b). Land is either used for agriculture (crops) or pastureland (animals), not both simultaneously. Biodiversity of threatened amphibians is more-or-less distributed throughout the country, although with high local heterogeneity (Fig. 1c); diversity of threatened birds is distributed throughout the country, especially on the coasts; biodiversity of protected reptiles is concentrated in the southern half of France, particularly in the "arc méditerranéen" (Fig. 1d, e). Tree diversity is highest in forest areas (Fig. 1f, Supplemental Material B).

We observe spatial variation in the distribution of carbon storage across the country (Fig. 2), with levels of carbon storage unsurprisingly

higher within forests (Supplemental Material B). However, we find large quantitative differences in the quantity of carbon stored between our carbon models (Fig. 2), the reason for which is grounded in the type of data used for the calibration of each model. The NDVI relationships are derived from urban forest (Myeong et al., 2006; Yao et al., 2014) or desert ecosystems (Amoatey et al., 2018); others, such as Gibbs et al. (2007) and Spawn et al. (2020) are derived from a variety of sources and ecosystems.

Net ecosystem productivity is mainly concentrated in forests, with its lowest values at higher elevations in the Alps and Pyrenees (Fig. 3a). Soil loss is similarly lowest at high slopes (Fig. 3b). Pollination potential is

quite high throughout the country (Fig. 3c, e), with some exceptions being along the coasts.[8] Pollination as measured by the percentage of suitable pollinator habitat follows forested areas (Fig. 3d, Supplemental Material B), with pockets of highly suitable habitat in mountain regions.

3.2. Within-service correlations

While there is certainly some debate about what level of correlation is meaningful for ecosystem services (Lee and Lautenbach, 2016), we interpret our correlations in a purely positive/negative mathematical way and prefer to focus on the trends in the results rather than their absolute values.

We find positive correlations between our measures of carbon (Fig. 4a-c), our measures of biodiversity as the number of threatened species and tree diversity (Fig. 4d), and pollination. (Fig. 4e). A notable exception is the negative correlation between trees and threatened birds, which is intuitive. We would expect diverse forests to be suitable habitat for bird species, and subsequently tree diversity to be inversely related to number of threatened or protected bird species. This example serves as a good reminder that our measures of amphibian, avian, and reptile diversity are the numbers of *threatened* or *protected* species. If we were using the *total* number of avian species in this case, then we would likely observe a positive correlation.

Overall, correlations are more-or-less constant as long as we sample more than ten percent of the landscape. Despite heterogeneity in the spatial distributions of biodiversity, carbon storage, and pollination, estimation of their interactions is robust to the sample size. In fact, it is only until we sample less than one percent of the data do we see variation in the mean spatial correlations – a claim that is confirmed by looking at the variance of our estimates (Fig. 4b, d-e).

Specifically for carbon storage, we find strong correlations between all measures, with mean correlation coefficients greater than 0.4 (Fig. 4c), even though their absolute value in tons/hectare differ. Qualitatively, these models give us similar information as to the spatial distribution of carbon storage across France. The fact that these models are correlated is expected. Forests, for example, will have a high carbon storage regardless if it is evaluated by a land use/land cover model or via plant reflectance. However, the quantitative degree to which they are correlated is another question. The NDVI methods are very strongly correlated to each other and robust to sample size, with mean correlation coefficients greater than 0.9 and variance close to zero regardless of the percentage of the landscape sampled, despite having quite different functional forms and parameter values.

3.3. Between-service correlations

Spatial correlations between ecosystem services are robust to sample size (Fig. 5). Mean interactions between ecosystem services are the same as long as we measure greater than ten percent of the landscape (Fig. 5a), and, for some services, do not change even when we sample less than one percent of the landscape. That is, the mean spatial correlation using fifty percent of the landscape is more-or-less identical to calculating the mean spatial correlation with ten percent of the landscape sampled. We see differences in the mean spatial coefficients only when randomly sampling less than ten percent of the landscape.

This result is confirmed when measuring the variance of spatial

correlations (Fig. 5b). As we decrease the proportion of the landscape sampled, the variance in the spatial correlation coefficient calculated across all samplings increases exponentially. By simple back-of-the-envelope calculations between the mean and the variance it can be illustrated that there are likely qualitative differences between sample calculations when we calculate the spatial correlation coefficient using a low proportion of the landscape. In other words, calculating the correlation coefficient using different small subsets of the landscape can yield both positive and negative values.

Expanding on our pairwise correlation coefficients from the previous section, agriculture was negatively correlated with all services except threatened amphibian biodiversity. Biodiversity of threatened amphibians was positively correlated with biodiversity of protected birds, reptiles, trees, and net ecosystem productivity, and negatively correlated with grazing, pollination, and soil loss. Interestingly, it showed mixed positive and negative correlations with our carbon models. Protected avian biodiversity was positively correlated with threatened reptile diversity, and negatively correlated with tree diversity, carbon, grazing, net ecosystem productivity, pollination, and soil loss. Biodiversity of threatened reptiles exhibited weak or positive correlations with most carbon models, positive correlations with tree diversity, grazing, pollination, and soil loss, and a weak negative correlation with net ecosystem productivity. Tree diversity showed positive correlations with all carbon models and net ecosystem productivity, and negative correlations with grazing and soil loss. It exhibited mixed correlations with pollination. Carbon models were positively correlated with net ecosystem productivity, but showed mixed correlations with soil loss and pollination. Grazing was positively correlated with all carbon models, net ecosystem productivity, pollination, and soil loss. Net ecosystem productivity was negatively correlated with soil loss, with mixed effects with pollination. Soil loss exhibited mixed, and often weak, correlations with pollination. Detailed figures of the trends within each ecosystem service can be found in Supplemental Material B.

4. Discussion

Data quality and quantity are two of the main limitations for estimating ecosystem services and ecosystem service management (Bennett et al., 2009; Crossman et al., 2013; Egoh et al., 2012; Hou et al., 2013; Layke et al., 2012; Martínez-Harms and Balvanera, 2012). We show that it is possible to obtain reliable estimates of the correlations between ecosystem services at the landscape level (the average correlation occurring across the landscape) when randomly sampling ten percent of the landscape for all ecosystem services studied, and close to one percent for some. Despite heterogeneity in the spatial distribution of ecosystem services, we only need to sample ten percent of the landscape to acquire an accurate measure of the average correlations between all ecosystem services at the landscape level.

To use the words of Mark Williamson (Williamson, 1996), our main finding is a type of "tens rule" applied to the statistical calculation of the spatial correlation coefficient.[9] Ten percent is the minimum proportion of the landscape that needs to be sampled in order to minimize variation in the calculation of the spatial correlation relative to the average correlation using the full sample. Below this level, variance in the calculation of the spatial correlation increases exponentially, and we also see variability in the calculation of the mean (Figs. 4 and 5). This result is at least partly a statistical phenomenon similar to general relationships between ecological process and spatial scale in ecology, such as the

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[8] Pollination potential exhibits a high degree of fine-scale spatial variation, much of which is lost when we aggregate the data. For example, the farthest distance from natural forest in our proximity analysis was 10.12 km. Aggregating the data to the 10x10 km resolution of the biodiversity data expectedly results in a loss of much of this information. However, we do see some variation in the pollination potential, though its overall values across the landscape are high. We would not expect this to affect the calculation of our spatial correlations.

[9] The tens rule from ecology is a statistical generalization of the establishment and spread of invasive species. It states that of the set of novel species introduced to a new local, ten percent are able to establish a self-sustaining population, and of those, ten percent become pests. For captive species, there is another initial step of ten percent of introduced species escaping captivity and becoming feral in the wild.
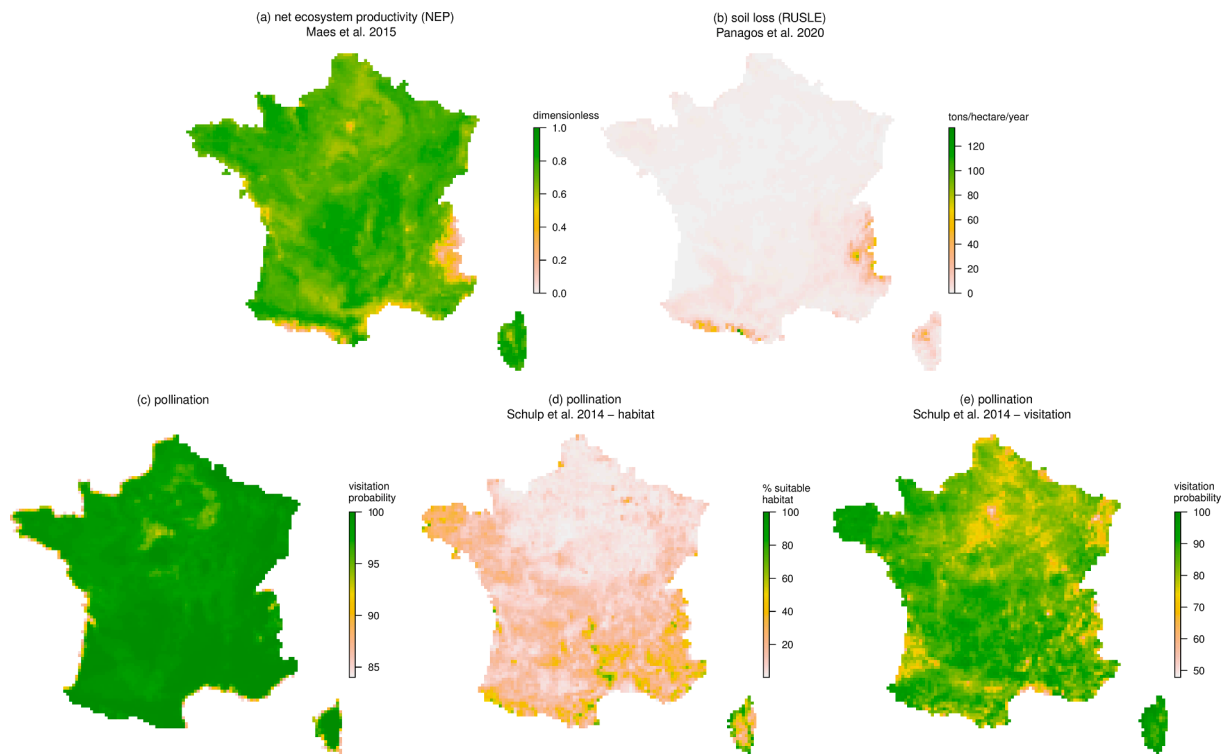
Fig. 3. Estimated ecosystem services: (a) net ecosystem productivity (dimensionless) (Maes et al., 2015); (b) soil loss (tons/hectare/year) (Panagos et al., 2020); (c-e) pollination. Note that the units for pollination are visitation probability (c, e) and the percentage of suitable pollinator habitat (d).

species-area relationship (SAR) (Arrhenius, 1921; Lomolino, 2000; Schoener, 1986), stability-area relationship (StAR) (Delsol et al., 2018), or relationships between biodiversity and ecosystem functioning (BEF) (Cardinale et al., 2011; Gonzalez et al., 2020). For each of these, the greater the spatial area studied, the greater the biodiversity (SAR), stability (StAR), or total community biomass (BEF). In our case, the greater the proportion of the landscape sampled, the lower the variation in the calculation of the correlation coefficients between ecosystem services.

As we increase the spatial scale of the analysis from very local to regional or national, we may change who, how, and how much parcels of land are managed (which will affect the underlying physical and biological processes occurring at each site) or exceed limits for species dispersal or pollination, both of which overall potentially change the driving factors for ecosystem service supply (Bennett et al., 2009; de Groot et al., 2010; Hou et al., 2013; Lee and Lautenbach, 2016; Millennium Ecosystem Assessment, 2005). From a purely statistical standpoint, increasing the sample size will minimize spatial heterogeneities in the data and, by consequence, variance in the calculation of the spatial correlation coefficients. Indeed, applying a measure of stability to the data – calculated as invariability or the ratio of the mean to the standard deviation (Shanafelt and Loreau, 2018; Wang and Loreau, 2016; Wang et al., 2017) – confirms this claim. Stability of the correlation coefficients increases exponentially as a function of the landscape sampled (Supplemental Material B), which is primarily driven by decreases in the variance (as opposed to increases in the mean), which approaches zero as the entire landscape is sampled. Thus, our "tens rule" is the threshold percentage of the landscape that minimizes variation in the calculation of the correlation coefficient. It is worth emphasizing that our threshold most likely directly applies to similar large-scale studies that use remote sensing land use and land cover data as proxies for ecosystem services. There are many ways to measure ecosystem services (Supplemental Material A), and other methods of data collection such as field surveys may not support the 10% sampling rate.

Our individual estimates of the spatial correlations between ecosystem services at the landscape scale are consistent with

expectations from the data and the models used to estimate them, and are in general agreement with the rest of the literature. For example, Raudsepp-Hearne et al. (2010) identified a consistent, negative relationship between agriculture and carbon sequestration. Mattison and Norris (2005), Phalan et al. (2011), and Reidsma et al. (2006) discuss the general negative relationships between agriculture and biodiversity. We find a positive correlation between agriculture and biodiversity of threatened amphibians, and negative relationships between agriculture and the number of threatened bird and reptile species. We attribute this to the fact that amphibians are most threatened by lowlands with agriculture (as opposed to pastoral highlands), and it is likely that more threatened amphibians will be located in agricultural areas. For protected birds and reptiles, we suppose that viable habitat for those species is either not used for agriculture or not as suitable for it compared to other land uses. (In contrast, if we were using the *total* number of species in each taxonomic group rather than the number of *threatened* species, we could expect to find the opposite signs of these relationships.) Many of our correlations are at least partially due to the nature of the data (discussed below), and we test only a small set of provisioning and regulating services. It would be interesting in future studies to test our findings across a broader set of ecosystem services, specifically a greater number of supporting and regulating services. Indeed, the literature has identified general trends in the trade-offs and synergies (positive or negative correlations) between broad types of ecosystem services (Lee and Lautenbach, 2016). For example, in a review of synergies and tradeoffs, Lee and Lautenbach (2016) found that synergistic relationships were more common between regulating services, and no-effect relationships between provisioning and cultural services.

While we would certainly express caution in interpreting our results in absolute terms, they do offer interesting questions for the management of ecosystem services and experimental design going forward. For example, when evaluating ecosystem service provisioning for urban development, what is the minimum amount sampling that is needed to effectively capture a landscape-level average measure of their interactions while still accounting for local heterogeneities? Given a
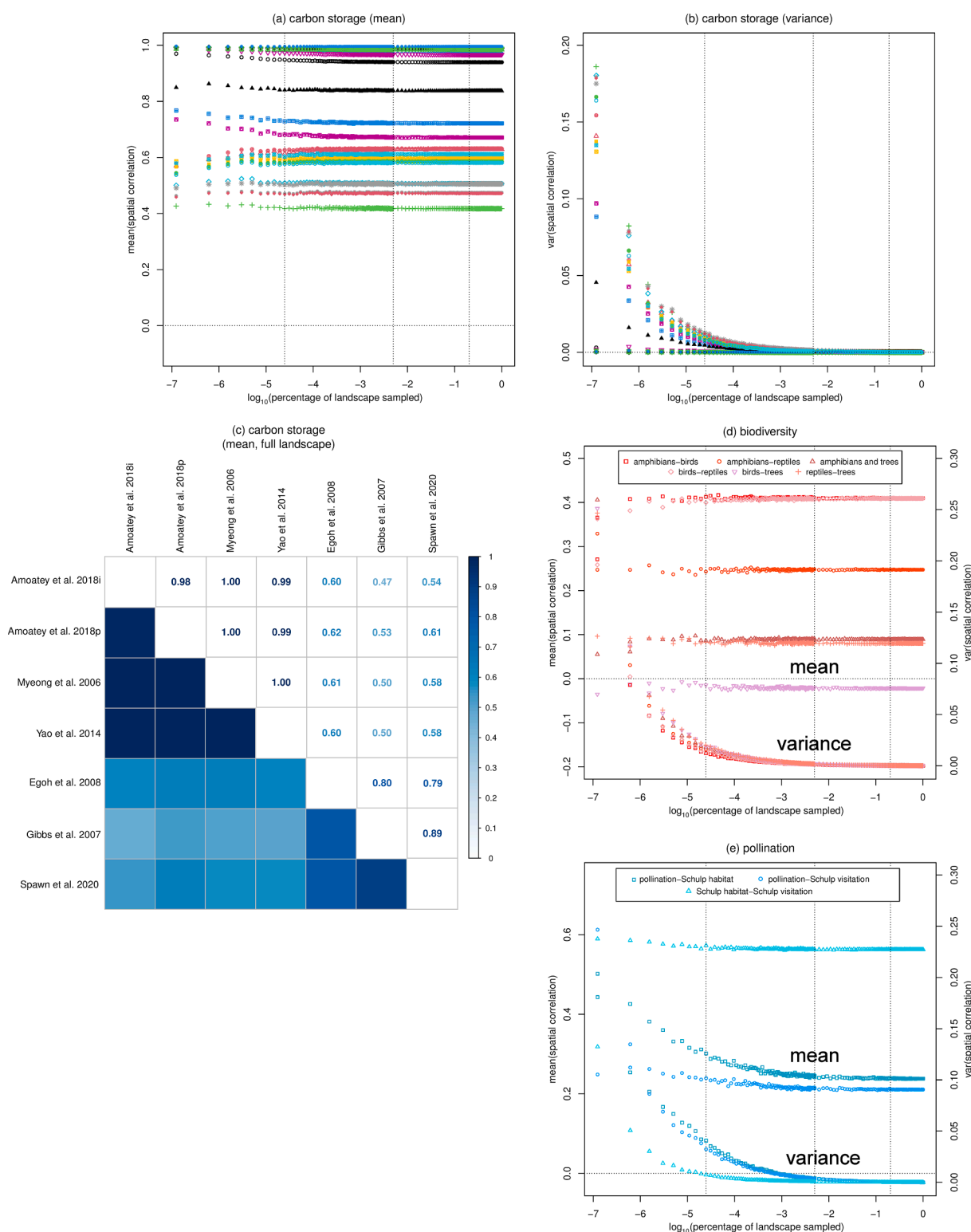
Fig. 4. Within-service spatial correlations for measures of carbon (a-c), biodiversity (d), and pollination (e). Mean and variance of carbon storage, biodiversity, and pollination as a function of the percentage of the landscape sampled are presented in (a-b) and (d-e) respectively. Note that these are meant to visualize the *trends* in the correlations as a function of the landscape sampled rather than the individual values of each pairwise correlation. From left to right, dotted vertical lines indicate one, ten, and fifty percent of the landscape sampled. Pairwise correlations between carbon storage estimates at the full landscape scale are given in (c). Values of each (row, column) combination are indicated by color and number.

sufficiently large sample size (discussed in more detail below), our "tens rule" would suggest a rate of greater than ten percent of the whole. Alternatively, we could flip the nail on its head by asking if fine-scale heterogeneities are important, what is the maximum amount of sampling that should occur to preserve this heterogeneity? We believe that this result could be useful in designing field surveys. For instance, if we were to randomly sample individual plots, sampling at the ten percent level would suffice; sampling above this would result in greater
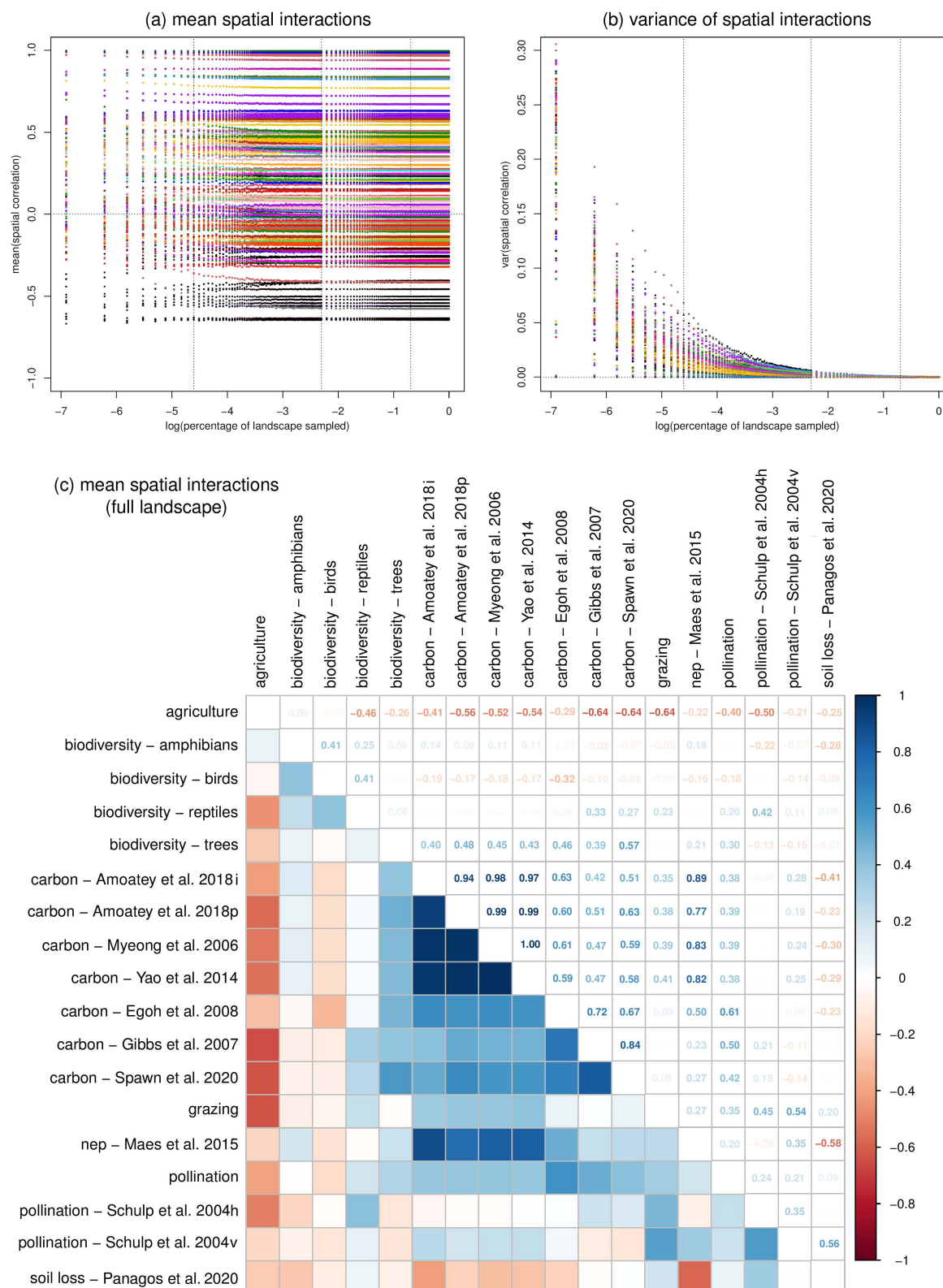
Fig. 5. Trends in the mean and variance of spatial interactions as a function of sample size (a, b), and mean spatial correlations at the full landscape scale (c). In (a) and (b), marker color and style indicate a correlation between two ecosystem services at a given proportion of the landscape sampled. Note that these are for illustration of the *trends* rather than identifying individual correlation coefficients. From left to right, dotted vertical lines indicate one, ten, and fifty percent of the landscape sampled. In (c), the qualitative (color) and quantitative (value) of the correlations are presented as pairwise (row, column) combinations of each ecosystem service, with the transparency of the numbers paralleling the strength of the correlation.

costs without yielding additional returns in terms of the mean correlation at the landscape level. Indeed, we would expect our "ten's rule" to hold even more strongly in homogeneous landscapes or sites of the same type or terrain, with even fewer data points being needed to estimate the average correlation occurring across the landscape. Our paper also offers a perspective for how we sample the landscape. In our study, we apply a random sampling approach with replacement. In reality, certain areas will be prioritized over others, with non-random sampling and spatial differences in sampling intensity (Brus, 2022; de Gruijter et al., 2006).

Particularly when making management decisions or environmental policies for heterogeneous landscapes, it is important to consider not only summary measures like the average correlation, but also the variation of correlations across the landscape. A country such as France, for example, contains a range of heterogeneous landscapes, each with different management profiles and bio-physical properties and processes, which can potentially lead to different ecosystem service correlations between them. It is certainly possible that the dominant correlation between two ecosystem services does not occur everywhere in the country. By comparing the mean and variances of our correlation coefficients across different sampling rates (Figs. 4 and 5), it is clear that it is possible for a correlation coefficient between two ecosystem services calculated from an individual sample draw to be qualitatively different from the average correlation calculated at the landscape level, particularly at low sampling rates. Summary measures have their place – it is useful to understand general relationships between ecosystem services, and establishing their common trade-offs and synergies is a frequent, reoccurring theme in the literature (Bennett et al., 2009; Lee and Lautenbach, 2016). But considering only the mean can hide variation that is averaged out during the aggregation process. Assuming that an association between ecosystem services occurs everywhere, and implementing a management policy at a large scale (regional or national), can likely lead to perverse outcomes.

One way to account for this is to break up the landscape into smaller subsections or ecoregions, and measure the correlations between ecosystem services at scales which preserve local heterogeneities that would be lost at larger scales. We subdivide the data into the thirteen political regions in France (Supplemental Material B) and re-run our analysis. Plots of the trends in ecosystem services and tables of correlation coefficients are found in Supplemental Material B. In general, we find that agreement between our estimates of correlation coefficients for all of France (Fig. 5) and at the full regional level (Supplemental Material B), though there are certainly differences particularly for regions with lower sample sizes such as Corse. Our "tens rule" holds reasonably well in most regions, but functions most generally across all regions in France at the fifty percent level. This highlights the potential role of sample size in driving the statistical phenomenon of minimizing the variance in the calculation of the correlation coefficients. Interestingly, the ten percent level of the national sample has more observations (533) than all but three regions (Auvergne-Rhône-Alpes, Nouvelle-Aquitaine, and Occitanie); the one percent level of the national sample is greater than the fifty percent level of the regions of Corse and Île-de-France. The threshold level for minimizing variation in the correlation coefficients likely varies from landscape to landscape as a function of landscape properties (e.g., heterogeneities in land use and land cover, management, soil properties and climate, etc.). Developing the contribution of each of these factors to the threshold requires a deeper statistical analysis across multiple landscapes and is left for future work.

Certainly, reliance on aggregated or proxy data and stylized models for estimating ecosystem services are a limitation to our study, but this is a general problem for this field of research (Crossman et al., 2013; Hou et al., 2013; Layke et al., 2012; Martínez-Harms and Balvanera, 2012). Take, for example, the relationships between agriculture, grazing, and the Gibbs et al. (2007) and Egoh et al. (2008) carbon models. Each ecosystem service is derived from land use and land cover data. Agriculture and grazing are calculated directly from the presence or absence of each respectively. The Gibbs et al. (2007) carbon model assigns an average storage of carbon by land use type, with forests and grasslands storing more carbon than agriculture; the Egoh et al. (2008) carbon model classifies carbon storage potential as "low", "intermediate", or "high" based on land use type. We would expect to find negative interactions between these three. Physically measuring ecosystem services in the field is time consuming and expensive, and other compartmental, phenomenological, or simulation models still require fine-scale data, much of which is not readily available. For instance, the Terrestrial Ecosystem Model (McGuire et al., 2001; Naidoo et al., 2008) and 3-PG tree growth model (Crossman et al., 2011a; Crossman et al., 2011c) both require local information on locally present species and management, as well as biophysical and weather data. Estimating recreation often involves conducting interviews or surveys to establish visitation rates (Tardieu and Tuffery, 2019). Air and water quality notoriously require point measurements of nitrogen and phosphorus inputs and removals, land use, hydrology, soil profiles, and weather (Bai et al., 2011; Guerry et al., 2012; Jansson et al., 1998; Maes et al., 2012; Nelson et al., 2009; Raudsepp-Hearne et al., 2010). For these reasons many studies rely on proxy data such as land cover, even though there are discrepancies between land cover-based proxy methods and actual fine-scale point measurement (Eigenbrod et al., 2010; Roussel et al., 2017). For example, Eigenbrod et al. (2010) found that models based on land-use data worked well for broad-scale applications but there were errors when applied to fine-scale resolutions. Roussel et al. (2017) found that finer-scale, phenomenological models were able to better account for local heterogeneities in service provisioning, leading to an identification of a greater number of clusters of ecosystem services than a lookup table model.

These ideas touch on a broader discussion of potential bias in the models used to estimate ecosystem service provisioning, and bias due to the structure of the data used by them. Firstly, in terms of biases inherent to models used to estimate the provisioning of ecosystem services, our analysis advises caution against interpreting estimates as concrete, ab-solute measures of ecosystem service supply and the blind application of proxy-based methods or benefits transfer. Our carbon models provide a straight-forward illustration of this. While they are quite positively correlated with each other (e.g., carbon hotspots in one model corre-spond to carbon hotspots in another), we find gross differences in the quantity stored between them, often of several orders of magnitude. The main reason for this is the type of data used in the calibration of each model. The NDVI methods rely exclusively on proxy data, being cali-brated to either urban forest urban forest (Myeong et al., 2006; Yao et al., 2014) or desert ecosystems (Amoatey et al., 2018). We would not expect these calibrations to perform well outside of urban areas or in temperate ecosystems. Other measures, such as Gibbs et al. (2007) and Spawn et al. (2020), are derived from a variety of datasets including forest inventories and expert opinion, and likely present a more accurate representation of carbon storage. However, that being said, our "tens rule" holds across all of the ecosystem services in this study – including external, published maps of ecosystem service provisioning – which is encouraging.

Secondly, it is possible that the structure of the landscape (the data) can potentially bias the calculation of the correlation coefficient. To illustrate this, let us focus specifically on land use-based estimates of ecosystem services. When randomly sampling the landscape, the land use type with the highest proportion will be greater represented in the sample, which can potentially impact the calculation of the correlation coefficient. (In contrast, a landscape with an even proportion of land use types will always return the same proportion in the sample on average and will be constant irrespective of the sampling rate.) Landscapes with one dominant land use type could be more or less likely to exhibit "bundles" of ecosystem services, which have been shown to occur be-tween certain types or groups of spatially autocorrelated ecosystem services (Bai et al., 2011; Raudsepp-Hearne et al., 2010). Thus, the physical structure of the landscape has a role in shaping the resulting correlations of ecosystem services. Very rarely do we find landscapes

with an even proportion of anything. There is almost always some heterogeneity, with landscapes being composed to greater proportions of a particular land use, micro-climates, soil conditions, etc. How should we account for potential biases caused by this in the analysis? On the one hand, we could try and control for it by restricting the analysis to regions with a more even proportion of land use types. But on the other hand, the data is the data, and in doing so we actually introduce bias to the analysis in the opposite direction. In a more traditional regression analysis, we would include a set of dummy variables that explicitly account for the effect of land use types in the data. This is not an option here. Perhaps this is a limitation of using the correlation coefficient to measure interactions between ecosystem services, as opposed to other methods such as linear regression, principle-components analysis (PCA), or production possibilities frontier (Feld et al., 2009; Lee and Lautenbach, 2016; Tardieu and Tuffery, 2019). One solution is to break up the data and explicitly test for potential differences caused by aggregations of the landscape, much like what we have done in our regional analysis (Supplemental Material B). Indeed, this approach is similar to general tests for bias caused by endogeneity in frequentist statistics (Angrist and Pischke, 2009; Cameron and Trivedi, 2005). We leave a comprehensive treatment of this to future work.

Our results indicate that it may be possible to reliably capture the value of an interaction between ecosystem services at low sample sizes – a hypothesis that could be tested empirically. The resolution of the data is fairly coarse, with a total of 5339 observations (pixels or study sites), which is comparable to smaller scale but finer resolution landscapes. At the national level, it should be feasible to obtain adequate sample sizes in the field to test our findings, particularly with larger, multi-lab collaboration networks (see, for example, the "NutNet" Nutrient Network, an ecological research network of over 130 grassland sites worldwide). Alternatively, it could be possible to exploit national plot data, such as the French National Forest Inventory (IFN) or the European Farm Accountancy Data Network (FADN). Future research could repeat our analysis at the local scale, using on-the-ground estimates of a broader range of ecosystem services. In this way, we can move away from binary ecosystem service measures, taking into account local heterogeneities in management, nutrient update/deposition, soil type, temperature, elevation, or precipitation.

Understanding how a measure of an interaction between services changes depending on the data type or quality is but one piece of the overall uncertainty puzzle. We believe that our study complements the existing literature and has important implications for landscape and ecosystem service management. We hope that it brings to light new questions previously unconsidered in the field.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data and scripts are available on the Open Science Framework (osf.io/7hk9v).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2023.101546.

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