

A quantitative framework for assessing spatial flows of ecosystem services



H.M. Serna-Chavez^{a,*}, C.J.E. Schulp^b, P.M. van Bodegom^c, W. Bouten^a, P.H. Verburg^b, M.D. Davidson^a

^a Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

^b Institute for Environmental Studies, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

^c Department of Ecological Science, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

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ABSTRACT

Spatial disconnections between locations where ecosystem services are produced and where they are used are common. To date most ecosystem service assessments have relied on static indicators of provision and often do not incorporate relations with the corresponding beneficiaries or benefiting areas. Most studies implicitly assume spatial and temporal connections between ecosystem service provision and beneficiaries, while the actual connections, *i.e.*, ecosystem service flows, are poorly understood. In this paper, we present a generic framework to analyze the spatial connections between the ecosystem service provisioning and benefiting areas. We introduce an indicator that shows the proportion of benefiting areas supported by spatial ecosystem service flows from provisioning areas. We illustrate the application of the framework and indicator by using global maps of provisioning and benefiting areas for pollination services. We also illustrate our framework and indicator using water provision and climate regulation services, as they portray important differences in spatiotemporal scale and process of service flow. We also describe the possible application of the framework for other services and other scales of assessment. We highlight how, depending on the ecosystem service being studied, the spatial service flows between provisioning and benefiting areas can limit service delivery, thereby reducing the local value of ecosystem service supply.

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1. Introduction

Ecosystem services comprise ‘the ecosystems conditions or processes utilized, actively or passively, to produce human well-being’ (MA, 2005; Fisher et al., 2009). The strict coupling in the definition of ecosystem services to human utilization has important consequences. First, there is a considerable difference between ‘potential’ and ‘actual’ service provision, since ecosystem conditions and processes only become services once they are actually used or consumed by human beneficiaries (Fisher et al., 2009). Second, there may be spatial dissimilarities between areas where

services are produced and where they are to be used. This implies that most ecosystem services are ‘delivered’ from provisioning to benefiting areas through either biophysical or anthropogenic processes. How the production connects with human beneficiaries is a crucial feature of the ecosystem service concept: the flow of services in space and time. To date, the use of the term ‘ecosystem service flow’ has been ambiguous, referring either to general service provision or to the path of delivery from providing to benefiting areas (e.g., Chan et al., 2006; Fisher et al., 2011; Bagstad et al., 2013). We define ecosystem service flows as the spatial and temporal connections between provisioning and benefiting areas. This definition centers ecosystem service flows as means for actual service provision (e.g., Reyers et al., 2010; Fisher et al., 2011; Turner et al., 2012) and, hence, complements the view of service provision to beneficiaries. Information on when and where benefits are enjoyed is required for designing and applying economic instruments, such as payments for ecosystem services (Wunder, 2007; Guariguata and Balvanera, 2009). For instance, the characterization of ecosystem service flows is crucial to identify key players in the efforts to mitigate climate change impacts through Reducing Emissions from Deforestation and Forest Degradation mechanisms (REDD+),

* Corresponding author at: P.O. Box 94248, 1090 GE Amsterdam, The Netherlands. Tel.: +31 0205257379.

E-mail addresses: h.m.sernachavez@uva.nl (H.M. Serna-Chavez), nynke.schulp@vu.nl (C.J.E. Schulp), p.m.van.bodegom@vu.nl (P.M. van Bodegom), w.bouten@uva.nl (W. Bouten), peter.verburg@vu.nl (P.H. Verburg), m.d.davidson@uva.nl (M.D. Davidson).

Agrawal et al., 2011). Additionally, the study of ecosystem service flows could highlight constraints as well as options to restore the delivery of services to beneficiaries, which is a key target of Action 2 of the European Union's 2020 Biodiversity Strategy,¹ and a strategic goal in the Convention on Biological Diversity's 2020 targets ('enhancing benefits from ecosystem services', Perrings et al., 2010).

To date, studies on ecosystem service flows are sparse and rather conceptual (Silvestri and Kershaw, 2010; Bastian et al., 2012; Syrbe and Walz, 2012). The temporal features of ecosystem service flows have rarely been addressed (e.g., Brauman et al., 2007; Bastian et al., 2012) and our understanding of the spatial features of service flows relies heavily on broad categories of the spatial relations between provisioning and benefiting areas (Costanza, 2008; Fisher et al., 2009). For instance, soil formation and erosion regulation are classified as *in situ* services, because providing and benefiting areas overlap completely. For storm and flood protection, service delivery depends on proximity (Brauman et al., 2007; Costanza, 2008; Fisher et al., 2009). For climate regulation, the delivery is global and omnidirectional (Costanza, 2008). Recently, Syrbe and Walz (2012) defined "the intervening space between non-contiguous providing and benefiting areas that influence process variables" as service connecting areas. This definition only indirectly addresses the spatial features of service flows and without quantification. This leaves a challenge quantifying the connections between ecosystems as service providers and the beneficiaries of those services.

Spatial assessments pairing provisioning areas with the corresponding benefiting areas can provide insights into the role of spatial flows in the delivery of a particular ecosystem service. Current mapping of ecosystem services has more often focused on the potential rather than the actual provision (e.g., Chan et al., 2006; Kienast et al., 2009; Haines-Young et al., 2012). Owing to the misrepresentation of actual provision and benefits, and the use of different input data and methodologies, considerable differences in the extent of ecosystem service provision and benefits are found among studies (Eigenbrod et al., 2010; Holland et al., 2011). The inclusion of the demand side, *i.e.*, the corresponding benefit and beneficiaries, is yet to become an integral part of assessments (e.g., Burkhard et al., 2012; Schulp et al., 2014). Only in a few regional-scale studies have the spatial features of ecosystem service flows been illustrated and estimated, e.g., indirectly, by mapping 'supply and demand' (Fisher et al., 2011; Burkhard et al., 2012), and directly by, e.g., estimating the perceived benefits from different forested areas to a given settlement (Palomo et al., 2012). At large scales the spatial connections between providing and benefiting areas for ecosystem services related to the trade in specific commodities, such as wood, fish and agricultural goods, have well been studied (Hoekstra and Hung, 2005; Deutsch et al., 2007; Kastner et al., 2011). The methodologies used to map and quantify the flow of such commodities, however, are only applicable for services that are marketable and tracked by international trade agencies.

A prominent study that explicitly used the spatial connections between providing and benefiting areas to evaluate spatial service flows is the one conducted by Turner et al. (2012). They examined how global ecosystem service values are realized and constructed spatial models of flow to estimate the population able to capture benefits. Their study makes an important step by explicitly modeling spatial flows to estimate the value of the delivered benefits. This approach, however, is difficult to extend and generalize to other applications given their agglomeration of individual spatial flows into coarse categories.

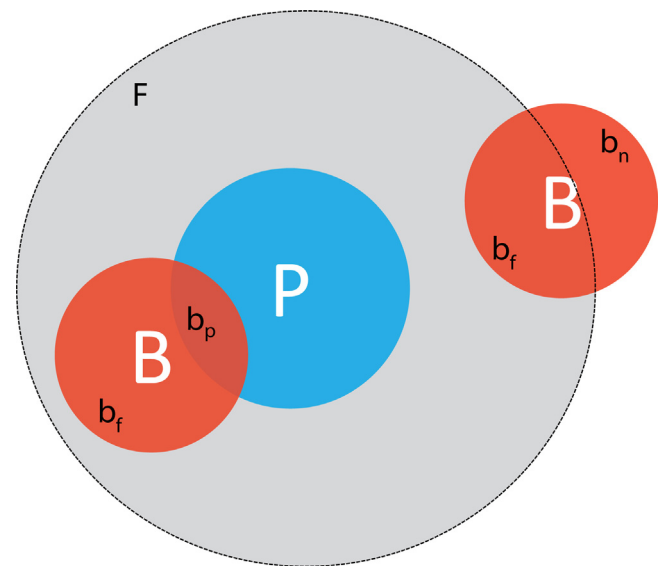


Fig. 1. Framework to analyze and quantify ecosystem service flows. Red circles with B, represent benefiting areas, while blue circle with P represents provisioning areas. F is the flow area within which services from provisioning area can potentially be delivered; b_f is the benefiting area not overlapping with P but within F; b_n is the benefiting area not-overlapping with the provisioning area and outside F; b_p is the benefiting area overlapping with the provisioning area.

In this article, we aim to assess the spatial flows of individual ecosystem services by mapping provisioning areas and the corresponding benefiting areas using a generic framework. Following this framework, we derive an indicator that characterizes the extent to which benefiting areas depend on spatial flows from other locations. We illustrate this approach by mapping, at the global scale, a number of illustrative ecosystem services that show distinctly different relations between provisioning and benefiting areas. Finally, we discuss how the framework can be applied in other settings to study the actual provision of ecosystem services.

2. Materials and methods

2.1. A generic framework to characterize and quantify spatial flows of ecosystem services

The framework we use to analyze the spatial relationships between ecosystem service providing and benefiting areas is illustrated in Fig. 1. The blue circle (P) represents a provisioning area, here defined as the spatial unit from which ecosystem services are sourced. The gray circle (F) represents the flow area, delineated by a maximum or threshold distance from the outer perimeter of the provisioning area (P) within which services can be 'delivered' to beneficiaries. Red circles (B) represent benefiting areas, defined as those spatial units in which ecosystem services are needed or readily used or consumed. The benefiting areas are further characterized as: b_p , the benefiting area overlapping with the provisioning area; b_f , benefiting areas not overlapping with the provisioning area but within the flow area (F); and b_n , the benefiting area not overlapping with the provisioning area and outside the flow area (F). An indicator for the importance of spatial flows for benefits from ecosystem services (*Ben.flow*) can be calculated as the ratio between the proportion of benefiting areas located within the flow area (b_f) and the total benefiting areas:

$$\%Ben.flow = \left(\frac{b_f}{b_f + b_p} \right) \times 100$$

¹ <http://ec.europa.eu/environment/nature/biodiversity/comm2006/2020.htm>.

Table 1
Spatially explicit data used to delineate ecosystem service provisioning and benefiting areas.

Service	Providing areas				Benefiting areas			
	Data (units)	Resolution	Year	Source	Data (units)	Resolution	Year	Source
Pollination	MODIS – continuous vegetation cover (% herbaceous and tree cover)	0.092° × 0.092°	2000–2001	Hansen et al. (2003)	Global distribution of agricultural crops depending or benefiting from pollination	0.092° × 0.092°	2000	Lautenbach et al. (2012)
	Global land systems map	0.092° × 0.092°	2000	Asselen and Verburg (2012)				
Water provision	Long-term average groundwater recharge rate (million m ³ year ⁻¹)	0.5° × 0.5°	1958–2000	Gleeson et al. (2012)	Annual groundwater abstractions (million m ³ year ⁻¹)	0.5° × 0.5°	2000	Gleeson et al. (2012)
Climate regulation	Above- and below-ground carbon density (Mg carbon ha ⁻¹)	0.5° × 0.5°	2000	Ruesch and Gibbs (2008)	Vulnerability of agricultural production to climate change (% change in total production)	0.5° × 0.5°	2000–2020	Wu et al. (2011)
	Top-soil carbon content (Mg carbon ha ⁻¹)	0.5° × 0.5°	2000	Hiederer and Köchy (2012)				
	Net ecosystem productivity (Mg carbon ha ⁻¹ year ⁻¹)	0.5° × 0.5°	2000	Sitch et al. (2003)				

High values for *Ben.flow* indicate: (1) a high importance of the spatial flows for the delivery of the service to the benefiting areas, and (2) a larger spatial segregation between provisioning and benefiting areas.

We present the application of the framework and indicator based on local-scale flows using biotic pollination services. The available knowledge on habitat requirements and foraging ranges of pollinators (Kremen et al., 2007), as well as the geographical location of crops benefiting from this service (Klein et al., 2007; Lautenbach et al., 2012), allows a comprehensive depiction of their spatial flows. The majority of ecosystem services, however, show important differences in their spatial characteristics of provision and flow. That is why, we also present the application of our framework using two other examples of ecosystem services where the connections between provisioning and benefiting areas are underpinned by different processes and operate at larger scales. These additional examples are only meant for illustration, for which we selected water provision and climate regulation services. For all ecosystem services we use global maps of provision and benefits (Table 1), delineating the flow area based on current knowledge (Table 2), and making assumptions matching global scale data availability. All analyses were conducted in ArcGIS v10.1. and R v2.15.2 (R Development Core Team, 2011) software.

2.2. Local-scale spatial ecosystem service flow: pollination

Provided to croplands by unmanaged pollinators, pollination services rely on the presence of suitable habitats (Kremen et al., 2007; Lonsdorf et al., 2009). The abundance of pollinators, and likely their contribution to effective crop pollination, decreases as isolation from suitable habitats increases (Ricketts et al., 2008; Garibaldi et al., 2011). To map provisioning areas at a global scale we used the percentage of vegetation cover in natural and semi-natural land cover categories as potential habitat for unmanaged pollinators. We used remotely sensed data on herbaceous and tree cover (MODIS,

Continuous Vegetation Cover; Hansen et al., 2003) within natural and semi-natural global land systems categories (Asselen and Verburg, 2012). These land system categories included dense forest, natural grassland, and mosaic cover of forest and grassland with extensive cropland or with few livestock. Herbaceous and tree cover within the other land system categories was assumed to be more intensively managed and, hence, unlikely to contain significant pollinator habitat. For the dense forest category, we only included forest edges in the vicinity of agricultural areas as part of pollinator habitat (Garibaldi et al., 2011). Forest edges were selected by neighborhood analysis, removing those cells entirely surrounded by the same land system category.

Local case studies have determined thresholds for habitat cover that enable optimal pollination to surrounding croplands (Kremen et al., 2004; Ricketts et al., 2008). Because of differences in spatial scales and types of data used, such thresholds could not be readily applied to our study. Therefore, we first assessed the relationship between tree and herbaceous cover and the cropland cover occurring within a distance of 2 km. The 2 km threshold was used since at greater distances visitation rates from unmanaged pollinators are likely to be negligible (Ricketts et al., 2008; Garibaldi et al., 2011). This assessment showed that with a tree and herbaceous cover of 45% most of the surrounding cropland areas (95% ± 5%) would occur within a distance of approximate 2 km (Appendix A). With the results, we refined the global provisioning areas of pollination services as those with tree and herbaceous cover ≥45% (hereafter ‘potential pollination habitat’).

Areas benefiting from pollination services were defined as those global areas where crops depending or profiting from biotic pollination are produced. These benefiting areas were delineated using a global map of the distribution of 60 crops depending or profiting, to varying extents, from pollination (Lautenbach et al., 2012). We then evaluated the extent of the spatial overlap between the provision and benefit maps (b_p). The spatial flow to non-overlapping, adjacent, cropland was evaluated by expanding

Table 2
Key ecosystem service provisioning and benefiting areas, and the spatiotemporal characteristics of flow among them.

Ecosystem service	Areas of ecosystem service		Flow		(Human) Benefits
	Provision	Benefits	Spatiotemporal scale	Process allowing	
<i>Pollination</i>	Natural and semi-natural habitats • Grassland • Shrubs • Heathland • Forest patches • Forest edges	Agricultural areas dependent on or profiting from biotic pollination	Rapid and local (range restricted)	- Foraging ranges of pollinator species - Pollen transportation and deposition - Abundance and effectiveness of pollinating organisms	- Direct: increased and/or realized crop yield - Indirect: intermediary in other services, e.g., reproduction of plants involved in climate regulation
<i>Water provision for irrigation</i>	Location of groundwater basins and their annual recharge	Agricultural areas dependent on groundwater irrigation	Basin-wide. Water availability is precipitation-dependent (seasonality)	- Infrastructure for extraction, distribution and irrigation - Basin recharge rate, which depends on: • Soil infiltration capacity • Topography	- Crop yield - Monetary
<i>Climate regulation</i>	Primarily, tropical (incl. peat forests) and boreal forest (hotspots)	Various Here: tropical, sub-tropical and mid-latitude agricultural areas vulnerable to changes in precipitation and temperature	Global non-excludable, and long-term (decades) Local-to-regional, and rapid (days, months)	- Vegetation and soil interactions with the atmosphere, such as: • Photosynthesis • Soil and plant evapotranspiration, soil heterotrophic respiration • Albedo • Plant aerosol production • Heat exchange - Global atmospheric mixing	- Avoided or ameliorated: • Decreased crop yields in tropical, sub-tropical and mid-latitudes • Decreased water availability • Increase in vector-borne exposure and water-borne diseases • Increased flood risk • Increased mortality from heat stress

pollinator habitat areas 2 km in every direction and re-evaluating the extent of spatial overlap with cropland areas (b_f).

2.3. Large-scale ecosystem service flows

2.3.1. Groundwater provision

To illustrate the analysis and quantification of regional-scale ecosystem service flows, we mapped groundwater recharge (i.e., provision) and abstraction (i.e., benefit) for crop irrigation following our framework (Fig. 1). As the aim of this particular example is not an exhaustive quantification of service provision and flow, we did not account for other technical solutions that influence the availability of water for irrigation, such as rain harvesting or the use of reclaimed wastewater. For groundwater provisioning and benefiting areas we used global maps of long-term recharge and abstractions for irrigation (in million m^3 year $^{-1}$; Gleeson et al., 2012), respectively. As these data are quantitative and of the same entity, we estimated to what extent groundwater recharge can meet abstractions for irrigation. We assumed that spatial flows of available groundwater to areas of abstractions occur only within basins, because transport of groundwater is constrained to within basins and to the presence of infrastructure for extraction and distribution. Only major groundwater basins, which are those with a mapped recharge rate > 2 mm year $^{-1}$ (BGR and UNESCO, 2008), were taken into consideration.

For each global groundwater basin, we analyzed the extent to which abstractions are covered by available recharge. This was calculated as the basin-wide difference between the average of abstractions and recharge, which represents the total of $b_p + b_f$. By doing this, all recharge is allocated to abstractions regardless the location of where both occurred. To illustrate the application of our framework for regional flows in more detail, we calculated the amount of abstractions for irrigation that can be covered by spatial flows of groundwater (b_f and *Ben.flow*) in three basins, i.e., the great plains (US), Ganges (India) and north China basin. The selected groundwater basins illustrate three different cases where b_f differs

in magnitude to meet abstractions for irrigation. For each basin, we used the average of recharge and abstractions to calculate the extent to which (1) recharge meets 'on-the-spot' (i.e., within the same grid-cell) abstractions (b_p), and (2) the remaining recharge available to flow within the basin (b_f). These two estimates were then used to calculate the *Ben.flow* for each of the three basins.

2.3.2. Climate regulation

The provision of climate regulation includes biogeochemical (e.g., carbon sequestration) and biophysical mechanisms (e.g., evaporative cooling) (Foley et al., 2003; Chapin et al., 2008). As quantifications of the biophysical mechanisms are scarce (Anderson-Teixeira et al., 2012), we only accounted for the stored and sequestered carbon in vegetation and topsoil as representative of a climate regulation service. For this purpose, a global carbon density map ($Mg\ ha^{-1}$) was constructed by adding the amounts of carbon stored in living vegetation (above- and below-ground; Ruesch and Gibbs, 2008) and in topsoil (0–30 cm depth; Hiederer and Köchy, 2012). From output of the LPJ-Dynamic Global Vegetation model (Sitch et al., 2003), we selected areas with a net ecosystem productivity (NEP, in $Mg\ ha^{-1}\ year^{-1}$) greater than zero, i.e., net additions to the terrestrial carbon pool. Areas within the top 25% quartile of the carbon density map were overlaid with the net sinks from the NEP map to delineate hotspots of provision. This hotspots map was used as provisioning areas of climate regulation and represents (1) areas of high above- and below-ground carbon density, (2) net carbon sinks, and (3) the areas where both overlapped.

Climate regulation services have a wide range of indirect and direct benefits, beyond off-setting anthropogenic carbon emissions. For illustration purposes, and because of a lack of global-scale maps of multiple benefits from climate regulation, we only considered agricultural production as a beneficiary. We used a map of agricultural production vulnerable to changes in temperature and precipitation under a business-as-usual climate change scenario (Wu et al., 2011). This map shows projected changes

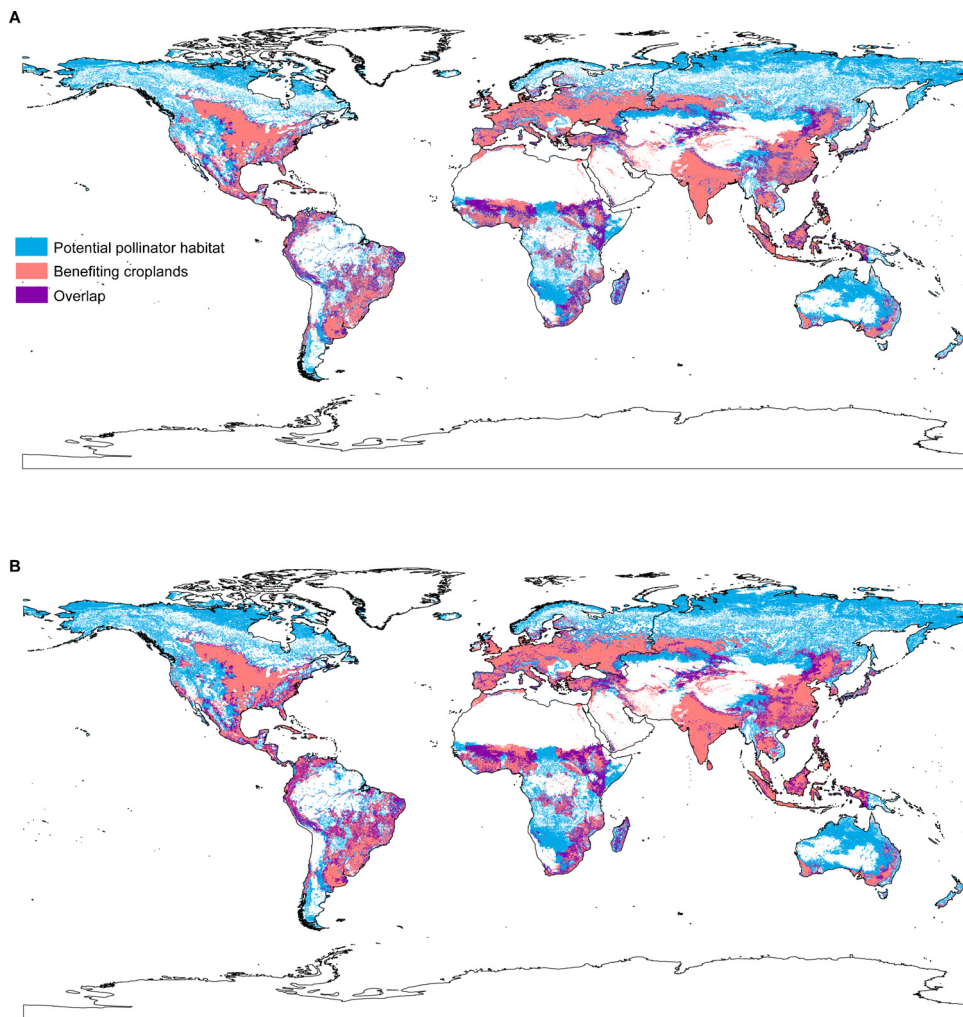


Fig. 2. Pollination service flow from potential habitat to cropland. (A) Spatial similarities between provisioning and benefiting areas (24.7%, b_p), which entails that within overlapping cells the potential habitat cover can enable pollination service flows to the surrounding croplands. (B) The increase in spatial similarities (31%, $b_p + b_f$) by accounting for the flow area for unmanaged pollinators to adjacent, non-overlapping, cropland areas. About 68% of the areas with crops profiting or depending on biotic pollination are outside the flow areas (b_n).

in total production of wheat, rice, soybeans and maize for the 2000–2020 period (as a percentage change in total production; (Wu et al., 2011)). These agricultural areas represent the production of four of the top-ten global agricultural commodities (FAO stats: <http://faostat3.fao.org/home>), which will benefit indirectly from the biogeochemical mechanisms of climate regulation. We only selected areas where a decrease in agricultural production is projected. To assess the proportion of benefiting areas depending on spatial flows of climate regulation services, we estimated the overlap between provisioning hotspots and benefiting areas (b_p). The flow area (F) for the delivery of indirect benefits through carbon sequestration and storage can be considered global (Table 2), thus all areas that do not overlap with provisioning hotspots (b_p), are within flow area (b_f). It is important to note, however, that in this case the service flow is indirect and that impacts of climate regulation may be spatially dependent.

3. Results

3.1. Local-scale pollination service flows

Of the global cropland areas that would benefit from pollination, 24.7% overlap with the provisioning areas (b_p). For these areas, the pollination service flows would occur within the area itself

(‘Potential service flow’ in Fig. 2A). Additionally, another 7.7% (b_f) is supported by pollination service flow (Fig. 2B). This last delineation of service flows assumes that the connectivity and distribution of habitat within the provisioning grid cells is sufficient to enable flows to adjacent open land cover with little or no pollinator habitat. Overall, this analysis indicates that 32% of the global pollination services delivered to croplands can be realized ($b_p + b_f$). About a quarter of this global services would be realized through spatial flows ($Ben.flow = 24\%$). This leaves about 68% of the global agricultural areas outside the flow area of unmanaged pollinators (b_n in Fig. 1). The regions where pollination flows from potential habitat are unlikely are the large-scale, homogeneous, cropland cover in, e.g., Midwest USA, and East Asia (Fig. 2B). These areas likely rely on artificial service provision by using, e.g., domesticated bee colonies.

3.2. Large scale spatial flows

3.2.1. Groundwater service flows

A global map illustrating the range of differences between groundwater abstractions for irrigation and recharge ($b_p + b_f$) and for all major groundwater basins in the world is presented in Fig. 3A. Groundwater basins in the arid regions of northern Mexico, Saudi Arabia and Iran display negative water balances, due to their

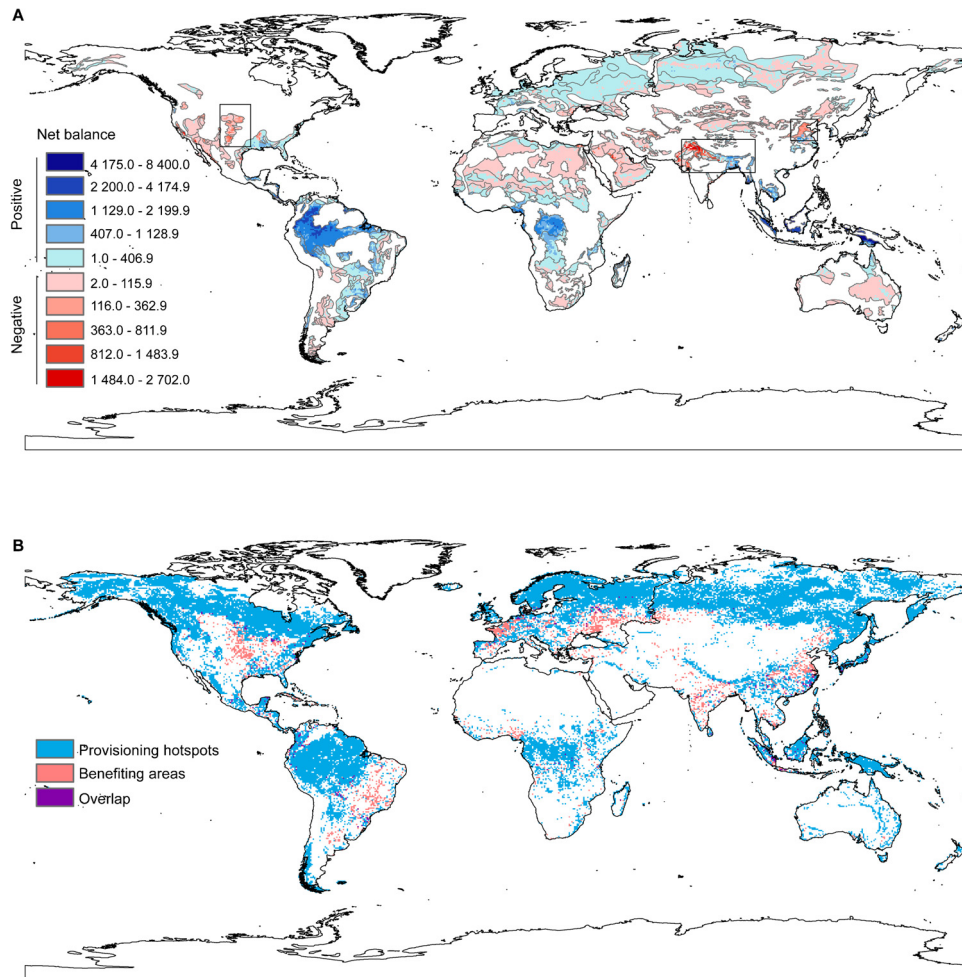


Fig. 3. Large-scale ecosystem service flows. (A) Groundwater provision for irrigation. Net basin-wide balance after average abstractions for irrigation were subtracted from the average recharge (million m³ year⁻¹). Results account for b_p and b_f , as all recharge is allocated to abstractions regardless their location. Temperate and mid-latitude regions show greater demands on service flows to fulfill the abstractions for irrigation. Boxes delineate the selected basins for detailed analysis of benefits through spatial service flows (in Table 3) (B) Global climate regulation service. Spatial connections between vulnerable agricultural areas and hotspots for climate regulation services. Overlap is considerable, with 21% of global agricultural areas overlapping with hotspots of provision (b_p), while the remaining 79% areas (b_f) rely on spatial flows.

low recharge rates and large abstractions. Groundwater basins in the Congo and Amazon regions display high positive net groundwater balances due to their high natural recharge and scarce abstractions.

Detailed examples of the calculation of *Ben.flow* indicator are given for three basins (Table 3). These basins differ in the amount of abstractions covered by overlapping recharge, and by spatial flows of recharge. The groundwater abstractions that are covered with ‘on-the-spot’ recharge (b_p) ranged from 7% to 82%, while the remaining recharge that would be able to cover additional abstractions (b_f) ranged from 2% to 21%. *Ben.flow* ranged from 10% to 75%. In all cases, a groundwater deficit remained.

Table 3
Ben.flow indicator and its components for three illustrative groundwater basins. Nomenclature after framework in Fig. 1.

Basin	b_p	b_f	% <i>Ben.flow</i>
USA high-plains	8%	2%	20%
Upper Ganges	82%	9%	10%
North China	7%	21%	75%

b_p : the amount of abstraction covered by ‘on-the-spot’ recharge.
 b_f : the amount of abstraction covered spatial flows of recharge.

3.2.2. Climate regulation service flow

The areas delineated as hotspots of provision of climate regulation services mainly comprise tropical and boreal forest areas (Provisioning hotspots in Fig. 3B). These forested areas are recognized as important biophysical and biogeochemical hotspots of global climate regulation (House and Brovkin, 2005). The benefiting agricultural areas show important clusters in central and Eastern Europe, China and the USA. Decreases in total production up to 88% are expected in these regions upon climate change (Wu et al., 2011).

The spatial disconnections between provisioning and benefiting areas are considerable, with only 21% of benefiting areas overlapping with provisioning areas (b_p , Fig. 3B). As agriculture generally does not provide climate regulation services, this overlap is likely due to the inclusion of a projected increase in total sown areas when evaluating future vulnerability of agricultural production (Wu et al., 2011). In this example all benefiting areas are within the flow area ($b_p + b_f = 100%$), given the non-rival and non-excludable characteristic of provision and flow (Costanza, 2008). Of the global benefiting areas, 79% of the benefits would be realized through spatial service flows (*Ben.flow*).

The spatial flows of climate regulation services are by way of global atmospheric connections, which entail no transport limitations. Given the time needed for atmospheric mixing (Meehl

et al., 2007; Bastian et al., 2012), the global benefits through carbon sequestration and storage by ecosystems are lagged in time. This is why the indirect global benefits from climate regulation services are segregated not only in space but also in time.

4. Discussion

4.1. A framework for ecosystem service flows

We introduced and illustrated a framework to characterize and analyze ecosystem service flows between provisioning and benefiting areas. We used pollination services and two other cases to illustrate key variations in the extent and location of benefiting areas as well as in spatial flows (Table 2). For these examples we used global-scale data to delineate ecosystem service provisioning and benefiting areas, using simplified representations of ecosystem service ‘supply’ and ‘demand’ that fit available data at this scale. We used pollination services to present the assessment of spatial flows following our framework (Fig. 2). By complementing the assessment of pollination service flows with the illustration of water provision and climate regulation flows, we were able to show how depending on the service analyzed, provisioning and benefiting areas can have intrinsically different characteristics, which implies that spatial flows are required to enjoy benefits from most ecosystem services. The spatial information needed to delineate provisioning and benefiting areas following our framework is readily available for most ecosystem services, which allows the extension of the study on spatial flows. In Table 4 we outline the application of the framework to different ecosystem services.

The generic framework we present builds on, and extends, the few studies that have explicitly illustrated or evaluated the spatial overlap between ecosystem service provision and benefits at landscape (e.g., Syrbe and Walz, 2012), regional (e.g., Fisher et al., 2011; Palomo et al., 2012), continental (e.g., Maes et al., 2011) or global scale (e.g., Turner et al., 2012). The framework is a parsimonious approach to study the spatial connections between provisioning and benefiting areas, and can be readily used for the majority of services given current data availability. The *Ben.flow* indicator provides a simple measure to identify the proportion of area where benefits are dependent on spatial flows. The calculation of the *Ben.flow* indicator depends on the delineation of a flow area (F in Fig. 1). This delineation of flow area allows the identification of those areas that depend on spatial service flows to enjoy benefits and is a first step toward the characterization and quantification of spatial flows and actual ecosystem service provision. The analyses here presented highlight how the flow area (F) is characteristic of each ecosystem service, and can be underpinned by the foraging ranges of mobile organisms (as in pollination), basin area and infrastructure (as in water for irrigation), or biophysical processes (as in climate regulation).

In the analysis of local-scale flows, unmanaged pollinators living in suitable natural and semi-natural habitats provide pollination services to nearby croplands. Given the spatial segregation between habitat and cropland (Kremen et al., 2007), benefiting areas are, by definition, completely dependent on pollination service flows from adjacent habitats. The study of service flows, therefore, requires accounting for a threshold distance from providing areas to identify the crop areas that can benefit from pollination services (*sensu F* in Fig. 1). For pollination, such information is available from field studies (Ricketts et al., 2008; Garibaldi et al., 2011). Here, we used such threshold distance to estimate the percentage of benefiting areas that are covered by spatial flows. The distinction between service flows that would occur in areas where both provision and benefiting areas can be found (b_p), and flows between adjacent provision and benefiting areas (b_f) but within the flow area (F) showed

how more than half the global cropland areas that would benefit from pollination are outside the flow area from potential habitats (Fig. 2). These features of spatial flow also highlight the possibilities for improving delivery to benefiting areas: by restoring or re-distributing habitat cover and its connectivity, or relocating the benefiting cropland areas.

To illustrate the characterization of spatial flows that operate at larger scales following the same framework, we used examples of water provision and climate regulation because they represent different processes underpinning provision and flow. In these two cases, ecosystem service flow is established through hydrological processes within groundwater basins and, indirectly, through the climate system, respectively. The irrigation infrastructure will affect the distance and direction (*sensu F*) that available recharge follows to meet abstractions. For our illustrative examples, we assumed that the installed infrastructure is able to deliver services throughout the basin to estimate $b_p + b_f$ for each global groundwater basin (Fig. 3A) and *Ben.flow* indicator in three cases (Table 3). For the indirect benefits from climate regulation services, there are known spatial and temporal segregations between provisioning and benefiting areas (Fig. 3B). In this case, the perceived benefits through carbon sequestration and storage cannot be attributed to a particular provisioning area (P), because of the flows through the global climate system, which makes the differentiation of benefiting areas into b_p or b_f not crucial. On the other hand, for the direct benefits of climate regulation through biophysical mechanisms, such as evaporative cooling (Foley et al., 2003), the neighboring provisioning areas (P) are likely the main contributors. The direct, smaller-scale, flows of climate regulation services were not included in our analysis, because a general maximum or threshold distance of a flow area (F) is not easily derived.

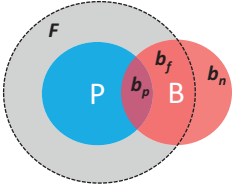
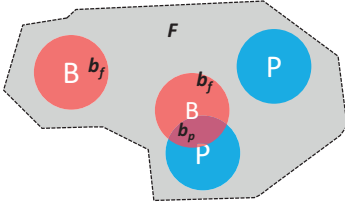
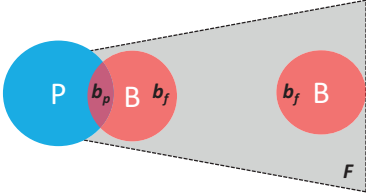
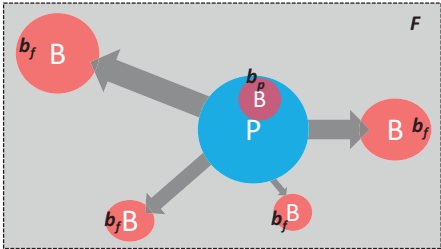
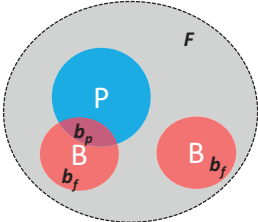
In this study we integrated all benefiting areas to analyze spatial service flows. As presented, the framework can also be applied to study the benefiting areas individually, which will then highlight those that rely more on spatial flows to benefit from ecosystem services. This characterization would consider the benefiting areas equally, regardless any difference in size or distance from the outer perimeter of provisioning or flow areas. The differentiation between benefiting areas would be attributed to the differences in overlap with provisioning areas (b_p), with the flow area (b_f) and, hence, in the *Ben.flow* indicator.

The framework may also be extended to the provision of multiple services, with known trade-offs and synergies. Such application would rely on the possibility to delineate a ‘common’ flow area and the identification of beneficiaries. In spite of the differences between ecosystem services, some do share key characteristics in their provision and spatial flow. For instance, the characteristics of provisioning, benefiting and flow areas for pollination services are similar to those for biological control (Thies and Tschardtke, 1999; Rusch et al., 2013), which facilitates the analyzes of both services with our framework.

4.2. Caveats and future research needs

A proper characterization and quantification of ecosystem service flows requires the identification of the spatiotemporal features in provision and flow, as well as the quantification of the processes involved. Our framework and indicator can serve as first approximation to evaluate the importance of spatial service flow (as in Fig. 2) and to quantify the delivered benefits (as in Table 3). The illustrations in this paper based on global data did, however, not explicitly address the individual flow paths between provisioning and benefiting areas. The ‘Service Path Attribution Network’ (SPAN) framework from the ‘Artificial Intelligence for Ecosystem Services’ project (ARES; Villa et al., 2009; Bagstad et al., 2013), helps

Table 4
Illustration of framework to evaluate spatial service flows to beneficiaries. Nomenclature of spatial service flow framework after Fig. 1.

Ecosystem services	F	b_f	b_p	b_n	p_a
<p>Pollination and biological control</p> 	Relative to the home and foraging range of the mobile organism(s) providing the service	Adjacent (non-overlapping) cropland areas, dependent on or benefiting from these services	Areas with both suitable habitat for providing agents and benefiting cropland	Dependent or benefiting cropland areas outside the flow area	Areas of suitable, natural and semi-natural, habitat
<p>Water provision for irrigation</p> 	Basin area	Areas with water abstractions and no or little water availability—rel. to natural recharge rates	Areas with both water availability—rel. to recharge—and abstractions	None, within a particular basin	Areas that experience natural groundwater recharge
<p>Moderation of extreme events and erosion prevention</p> 	Areas between the extreme event and the benefiting areas, e.g., for erosion prevention, upland vegetated areas as there is a slope-dependent relationship	Areas of settlements or infrastructure vulnerable to extreme events	Areas with both provision and benefiting settlements or infrastructure	Depends on degradation processes considered	Area, natural or semi-natural, that buffers extreme events or prevents soil erosion, e.g. wetlands, floodplains and reservoirs can buffer floods
<p>Provision of food and raw materials</p> 	Delineated by anthropogenic processes of storage, commercial trade, as well as demand	Areas where the exported production is delivered	Domestic consumption or use	Demanding or necessity areas that cannot import	Total production
<p>Climate regulation</p> 	Global	Areas that do not overlap with provisioning—high carbon density or carbon sink—areas	Areas that both provide and benefit from climate regulation	None	Areas with high carbon density and net carbon sequestration rates

connecting biophysical measures of service provision with human use and consumption, by connecting both spatial locations. SPAN also includes models of spatial flow and allows an approximation on the uncertainty of service provision and value of benefits (Silvestri and Kershaw, 2010; Logsdon and Chaubey, 2013). This approach, explained in Bagstad et al. (2013) remains data- and knowledge-intensive, which strongly limits its applicability at large scales and for many ecosystem services and areas where relevant data is not available.

To help improving the analysis of spatial flows we suggest building future extensions following landscape metrics. For instance, landscape proximity and connectivity metrics can help assess

which benefiting areas rely on which provisioning areas for the delivery of services, given a defined distance from provisioning areas (F). The latter can also help assessing the permeability and resistance to service delivery, as such complementary landscape metrics can consider the constraints posed by defined anthropogenic or natural barriers within a given spatial flow area.

Coupled to the spatial service flows that can be assessed with our framework, there are key temporal features of service provision and flow. To date, explicit recognition of temporal features of provision and flow is only slowly emerging (Brauman et al., 2007; Bastian et al., 2012), and such features are yet to be integrated in ecosystem

service assessments (Brown et al., 2005; Koch et al., 2009). The integration of temporal features into assessments is not readily supported by available frameworks given also the vast differences in temporal features among ecosystem services (Rodriguez et al., 2006). Some understanding on the temporal features, however, may be obtained from the processes determining the service flows, as analyzed in our framework. For instance, local-to-regional benefits of climate regulation, as influenced by water and energy exchanges between vegetation and atmosphere, are experienced rapidly, within days to months basis (Pielke et al., 1998). On the other hand, the global indirect benefits through the modulation of atmospheric concentrations of greenhouse gases are segregated from provision in time, given the time required for atmospheric mixing (Pielke et al., 1998; Meehl et al., 2007). To illustrate this, we highlight the importance of the delineated provisioning hotspots (Fig. 3B), based on average NEP, as past, present and future service providers. The hotspots are *past* service providers, for the processes that lead to high carbon densities in living vegetation and soils; *present*, for the continuation of sequestration and the stability of current carbon stocks; and *future*, since the long-term stability of the terrestrial carbon pool, and fluxes of energy and greenhouse-gases can mitigate, or ameliorate, some of the expected impacts of global climate change. Acknowledging as well as accounting for these temporal features of climate regulation services, as well as for any other ecosystem service, is key to assess the actual benefits from ecosystems. Table 2 describes the temporal characteristics of flow for the ecosystem services discussed in the paper.

The delivery of ecosystem services and the links between provisioning and benefitting areas as quantified in our framework also has a critical socio-ecological dimension. Therefore, it represents a key component to make the ecosystem service concept operational (Kremen and Ostfeld, 2005; Nicholson et al., 2009). This is illustrated in a study on ecosystem service flows provided by Palomo et al. (2012). They identified and estimated the amount of ecosystem services perceived as such by the local population surrounding a national protected area and other forested areas. They explicitly used the concept of ecosystem service flows to illustrate the extent to which benefitting areas enjoyed services from neighboring and distant providing areas. In this case accounting for ecosystems service flows helped to support the design of better management approaches, evaluation of trade-offs and informed decision-making by determining where the services from a provisioning area are being delivered to particular beneficiaries (Guariguata and Balvanera, 2009; Silvestri and Kershaw, 2010; Crossman et al., 2013). We envision that the quantification of ecosystem service flows, as provided by our framework, may aid supporting decision making in similar settings elsewhere.

5. Conclusions

The analyses in this paper highlight how the spatial characteristics of the flow between provisioning and benefitting areas are specific to each service. The study of ecosystem service flows requires guidelines for assessments that are appropriate for all services as well as all spatial scales. The generic framework for analysis of spatial flows of ecosystem services, as presented in this paper, can be a first basis to support such assessments. Understanding the spatiotemporal characteristics of production, flow and delivery to beneficiaries, and accounting the processes pinpointing them, are crucial to make the ecosystem service concept operational. Our framework may aid the evaluation of options to restore or improve the delivery of benefits now and in the face of global environmental and land-use change. The study of ecosystem service flows is key in assessments aiming to design economic instruments based on actual service provision, and for the characterization and

management of geopolitical disparities between service providers and beneficiaries.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2013.11.024>.

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