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Linking landscape structure and ecosystem service flow

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ABSTRACT

Despite advances in understanding the effects of landscape structure on ecosystem services (ES), many challenges related to these complex spatial interactions remain. In particular, the integration of landscape effects on different components of the service provision chain (supply, demand, and flow) remains poorly understood and conceptualized. Here we propose a theoretical framework to further explore how the spatial flow of ES can vary according to landscape structure (i.e. composition and configuration) emphasizing the role played by the configuration of supply, demand, and neutral areas, as well as individual characteristics of ES (e.g., service rivalry). For this, we expand the discussion on how landscape changes can affect ES flows and propose a theoretical representation of ES flows variation led by different supply-demand ratios. Additionally, we expand this discussion by integrating the potential effects of neutral areas in the landscape as well as of supply/demand spatial overlap. This novel approach links the spatial arrangement (e.g. fragmentation, network complexity, matrix resistance) usually captured by landscape metrics, and ratios of ES supply and demand areas to potential effects on spatial flows of ES. We discuss the application of this model using widely studied ES, such as pollination, pest control by natural enemies, and microclimate regulation. Finally, we propose a research agenda to connect the presented ideas with other prominent research topics that must be further developed to support landscape management targeting ES provision. The prominence of ES science calls for contributions such as this to give the scientific community the opportunity to reflect on the underlying mechanisms of ES and avoid oversimplified spatial assessments.

1. Introduction

Intense human-induced landscape modification, mostly led by urbanization and agricultural land use change (including expansion), alternates ecosystem conditions and directly affects biodiversity and ecosystem functions (Johnson et al., 2017; Maxwell et al., 2016). Consequently, the provision of ecosystem services (ES) that sustain human well-being has declined globally (IPBES, 2019). However, increasing human population size is accompanied by higher demands for the resources and functions provided by these ES, such as food, water, energy, climate, and water regulation (de Amorim et al., 2018; de Fraiture and Wichelns, 2010; Godfray et al., 2010). Therefore, effective

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landscape management is required to guarantee the sustainable use of environmental assets, maintain adequate levels of ES provision, and safeguard equity in access of environmental benefits (Berbés-Blázquez et al., 2016; de Groot et al., 2010).

Within the landscape management perspective, ES provision is conceptualized as arising from the interaction of three components of the service provision chain (Burkhard et al., 2014; Moreira De Lima et al., 2009; Schröter et al., 2018; Tallis et al., 2012; Villamagna et al., 2013): a) supply, as the ecosystem capacity or potential to provide a given service (Tallis et al., 2012); b) demand, as the service needed, desired or required by people (Villamagna et al., 2013); and c) flow, as the transfer of the benefit between supply and demand, and thus dependent on the mechanisms that connect supply and demand (Metzger et al., 2021a). While natural sciences embrace the supply side of the service provision chain (Martínez-Harms and Balvanera, 2012), broader participation of social sciences has further developed the demand side (Wolff et al., 2017; Wolff et al., 2015; Peter et al., 2022). On the other hand, an interdisciplinary approach between economics, natural, social, and cultural sciences has been fundamental in integrating ES components and addressing ES flows (Baró et al., 2016; Felipe-Lucia et al., 2015; Geijzendorffer et al., 2015; Palomo et al., 2013; Schröter et al., 2018; Felipe-Lucia et al., 2022). This is mostly because ES flows vary from geophysical and ecological processes (e.g., air mass movement for air pollution filtering; the movement of organisms for pollination; de la Barrera et al., 2016; Grote et al., 2016; Medeiros et al., 2019) to cultural identity (e.g., symbolism related to nature bonding; Fish et al., 2016; Schirpke et al., 2018), human agency and economic transactions (e.g., crop transportation and markets; Yu et al., 2013).

In relation to the demand component of the service provision chain, there is evidence that demands for multiple ES directly or indirectly drive landscape modifications (Willemen et al., 2012; Neyret et al., 2023). These drivers usually manifest in the form of economic pressures from crop and animal production, and industry resulting in land-use change (Curtis et al., 2018; von Haaren et al., 2019). For example, food production and international trade are the main drivers of forest loss worldwide (Curtis et al., 2018). As a result of increasing provisioning services linked to agriculture, several regulating services supplied by natural areas are threatened without being accounted for (e.g., flood control, water and disease regulation, and carbon storage). To avoid ES loss several attempts to manage land use and reduce undesirable changes emerge in the form of policies, governance, or market instruments (Metzger et al., 2021b), for instance the creation of protected areas or the use of Nature-Based Solutions. However, most attempts do not rely on spatially explicit designs that take into consideration the interactions between landscape components that will impact ES flow.

The consolidation in the definition of ES flow is an ongoing process. Most research dealing with ES flow addresses it similarly, despite some slight variation in definition and the term used to name it (Wang et al., 2022). Some studies address the spatial flow of ES by dealing with spatial matches and mismatches between supply and demand areas (Palomo et al., 2013; Geijzendorffer et al., 2015; Ortiz et al., 2018; Schirpke et al., 2019a), while some use different terms such as "actual use" of ES (Schröter et al., 2012), or "match" between ES demand and supply (Schulp et al., 2014) to refer to flows. Others emphasize the flows of matter or organisms that connect supply and demand areas (Metzger et al., 2021a). There are also cases in which ES supply and demand areas are very far apart, which has driven to a broader understanding of decoupled ES situations, and, therefore, international, or interregional flows have become more explicitly addressed (see Kastner et al., 2011; Koellner et al., 2019; Schröter et al., 2018). Despite relevant advances from studies that deal with ES for which supply and demand occur within a landscape (hereafter "coupled" ES), the understanding of how landscape structure, both in landscape composition (i.e., the types of existing elements or land uses) and landscape configuration (i.e., how these elements are arranged in space), affects their flow is still shallow (Metzger et al., 2021a).

Landscape structural effects on ES provision are context dependent (Hodder et al., 2014; Inkoom et al., 2018; Liu et al., 2017), and landscape structure has commonly been quantified based on habitat loss and fragmentation, landscape complexity, spatial heterogeneity, and connectivity (e.g. Duarte et al., 2018; Lamy et al., 2016). However, several distinct metrics have been used to quantify such variation, thus, hindering comparison between studies (Duarte et al., 2018; Fahrig et al., 2011; Laterra et al., 2012; Mitchell et al., 2015a; Mitchell et al., 2013). Some generalizable patterns in ES response to landscape configuration have been synthesized, but mostly referring to ES supply (e.g. Duarte et al., 2018; Lamy et al., 2016; Mitchell et al., 2013; Verhagen et al., 2016). For instance, Mitchell et al. (2015b) made a theoretical proposition about the effects of landscape fragmentation *per se* (*sensu* Fahrig, 2003) on ES supply and flow, without explicitly accounting for ES demand. However, the understanding of ES flow, especially for "coupled" ES, depends on the recognition of demand areas (Serna-Chavez et al., 2014), thus making it necessary to account for both the supply and demand components to fully assess landscape structural effects on ES flow.

Despite being fundamental, more research is needed to understand how landscape structure and the spatial distribution of supply and demand modulate ES flows, especially when considering configurational effects (Metzger et al., 2021a). Furthermore, the assessment of ES requires a clear identification of supply and demand areas, but more has to be done to include neutral areas (i.e. areas that are not characterized as supply or demand for the given ES). Neutral areas are composed of other types of land uses and have a role in spatially connecting supply and demand, thus enabling or hindering ES flow. Additional characterization of such neutral areas will depend on the ES being studied (once ES flows are specific for each ES). Only then we can have a better understanding of how to meet existing demands by assuring ES supply and promoting ES flow.

In this paper, we address this research gap by theoretically exploring how the spatial flow of ES could vary according to landscape structure (composition and configuration), emphasizing the role played by configuration (Section 2). For this, first, we build on the idea proposed by Mitchell et al. (2015b) and expand the discussion on how different landscape changes (other than fragmentation *per se*) can affect ES flows (Section 3.1). Second, we propose a theoretical representation of how ES flows could be affected by different supply and demand ratios (Section 3.2). Third, we expand this discussion by acknowledging that spatial flows are usually passing through neutral areas. Therefore, we integrate neutral areas in the landscape composition (Section 3.3) and explore the supply/demand spatial relationship including supply/demand overlap (Section 3.4). Lastly, we propose a research agenda to connect the presented ideas with other prominent research topics that must be further developed or integrated to support landscape management for ES provision (Section 4). The co-production of ES and their temporal variation are out of the scope of our proposal.

2. Approach and conceptual framework

The conceptualization of this framework was initially developed in a set of workshops aimed at discussing processes "Linking Landscape Structure to Ecosystem Services", held as part of a larger multidisciplinary collaboration between Brazilian and Australian research institutes. The focus of the workshops was to promote collaboration among the participants and advance the understanding of the relationship between landscape structure and the components of the service provision chain (supply-flow-demand), following a synthesis approach (Halpern et al., 2020). Relevant outcomes emerged from this international collaboration: a theoretical exploration of the spatiotemporal dimension of supply, flow, and demand (Boesing et al., 2020); and a review of the effects of landscape-level processes on ES complemented by a framework to improve the integration of landscape effects on ES assessments (Metzger et al., 2021a). Next to those, in this paper, we further explore landscape effects on ES flow and propose a theoretical representation of the relationship between supply, flow, and demand.

From the extensive discussions carried out in the workshop, the authors first established a ‘common’ terminology to enable the development of a deeper understanding of how landscape influences ES. Therefore, a clear yet synthetic definition of common terms related to ES was a fundamental starting point. Given the varying understandings of those terms in this consolidating field, a Glossary was organized to present the concepts to those less familiar with the field, and to clarify how we approach them to those who might have a distinct understanding (Section 2.1). Secondly, we employed a snowballing approach to search the literature, combining backward and forward snowballing (Jalali and Wohlin 2012), targeting papers dealing with landscape configuration effects on ES and focusing on ES flow, using key papers as a starting point (i.e. Mitchell et al. 2015b; Metzger et al. 2021a). The literature was used to contextualize the discussions and elaborate a set of examples used to illustrate the proposed ideas. We acknowledge this was not an extensive systematic literature review. Thirdly, a schematic representation of the conceptual framework including the links between landscape composition and configuration and the components of the service supply chain helped framing the discussions (Fig. 1). This framework can be considered as a “boundary concept” or “boundary object”, facilitating the integration of knowledge from different authors (Schröter et al. 2023). Multiple discussions were carried out after the workshop mostly among the authors and subsets, but also in informal consultation with other interested peers. In this way, the construction of the theoretical representations, illustrations, and examples presented here emerged from dialogue and the collective understanding of the complex processes underlying the relationship between landscape and ES.

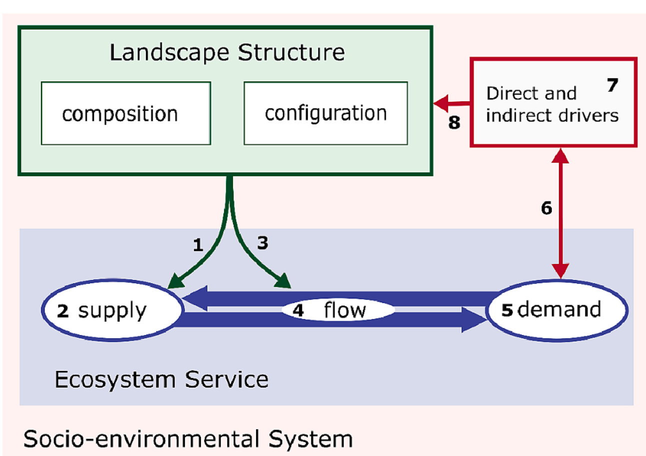

Fig. 1. Ecosystem Service framework highlighting the link between landscape structure and the components of the service provision chain. Landscape structure (both composition and configuration) can directly influence the condition of ecosystems (1) (e.g., their amount in the landscape or the quality of ecological processes within them) and, therefore, their capacity to supply ES (2). Landscape structure can also modulate the actual flow of ES (3), shaping their intensity and amount (4). The demand fulfillment depends on the flow of ES and the conversion of ES supply into a benefit for humans (5). We argue that demand is mostly influenced by social aspects (6) and can be one of the indirect drivers (7, 8) of changes in landscape configuration and composition. Other direct drivers (8) such as climate change, infrastructure development, and urban expansion, can also lead to landscape modification. Similarly, political and economic instruments (7), like Payment for Ecosystem Services (PES), can be used to manage landscapes (8) with the purpose of increasing benefits to people via supply enhancement (1) or flow facilitation (3).
Adapted from Mitchell et al., 2015b

2.1. Glossary

Service Provision Chain: parts of ecosystem service realization that generate benefits to people from ecosystems (Tallis et al., 2012). These components consist of the ecosystem service supply and demand areas connected through ecosystem service flows (Metzger et al., 2021a).

Ecosystem Service Supply: the potential of an ecosystem to provide an ecosystem service irrespective of being used, recognized, or valued by humans (Mitchell et al., 2015b; Tallis et al., 2012).
Even though ES supply per spatial unit may vary according to the ecosystem type and its condition, here we refer to supply as the area of the ecosystem that has the potential to supply a certain ES, without accounting for such variation.

Ecosystem Service Flow: It can be defined in physical terms as any flow of matter or organisms that connects supply and demand areas (Metzger et al., 2021a). However, in some cases ES provision relies on the interruption or reduction of spatial flows (e.g. flood regulation; Metzger et al.2021a). ES flow characteristics and mechanisms are specific to each service (Serna-Chavez et al., 2014).

Ecosystem Service Demand: the amount of service required or desired by people (Villamagna et al., 2013; Wolff et al., 2017; Wolff et al., 2015), even in cases in which they are not aware of such needs. ES demand can be expressed in terms of risk reduction, preferences and values, direct use or consumption of goods and services (Brander and Crossman, 2017; Wolff et al., 2017; Wolff et al., 2015). In some cases, the demand is not directly from people (e.g. from a crop dependent on pollination, but that eventually benefits a farmer). Here we assume the demand area as the location of people who require or desire the ES in question despite variations between these areas, such as population, or cultural differences

Ecosystem Service Provision: the delivery of a service to be used or enjoyed by people (Mitchell et al., 2015b; Villamagna et al., 2013). According to Metzger et al. (2021a), this term has been used in the literature with simplified approaches in which provision is inferred only through supply or when it only matches the flow (as the realized service); in several cases, it does not consider all the components of the service provision chain.

Benefit: positive change in people’s well-being (Tallis et al., 2012) as a result of ES provision.

Neutral Area: an area in the landscape that is neither supply of nor demand for the ES in question, but that can affect ES flow (i.e. facilitate or hinder it).

Ecosystem Service Rivalry and Excludability: To be rival means that the use of an ecosystem service by one person precludes the use of it by another person (Fisher et al., 2009). To be excludable means that one person can keep another from using or accessing an ecosystem service (Fisher et al., 2009). Marketed goods are usually rival and excludable; however, it is possible to fit ecosystem services along a continuum from rival to non-rival and from excludable to non-excludable.

Decoupled (and coupled) Ecosystem Services: *decoupled* ES is when the supply of and demand for an ES occur at different spatial scales or landscapes (Burkhard et al., 2014; Fisher et al., 2009). Inversely, here we use *“coupled” ES* when an ES has its supply and demand occurring within the same landscape. In this case, the spatial relationship between supply and demand has been previously classified as in situ, omnidirectional, and directional by Burkhard et al. (2014).

Ecosystem Condition: refers to the integrity and state or functioning of an ecosystem, ultimately determining its capacity to supply ES (Burkhard and Maes, 2017; UN, 2014).

Landscape Structure: spatial composition (the types of existing elements) and configuration (how they are arranged in space) of the landscape (Wu, 2013).

Supply and Demand Ratio: the proportion between the amount of ecosystem service supply area and the amount of ecosystem service demand area, here considered for "coupled" ES. Even though we acknowledge the existence of variation in supply and demand per area unit, here we do not take this variation into account.

3. Linking landscape structure and service flows: Proposing a theoretical framework

3.1. How landscape changes affect ES flows

ES flows, particularly those of coupled ecosystem services, are modulated by the spatial arrangement of ES supply and demand areas. Therefore, identifying and mapping such areas is a first step to start exploring which are the mechanisms that enable ES to flow between supply and demand areas within landscapes. Further, understanding whether the spatial flow depends on specific landscape structure is crucial to identify which landscape metrics to account for (Metzger et al., 2021a). For instance, the flow of regulating services like pollination and biological pest control within agroecosystems depend on the effects of the landscape on animal communities and their ability to move between their primary habitat areas and crops (i.e. spillover; Saturni et al., 2016). Landslide prevention, depends on erosion surface and rainfall runoff, strongly influenced by the spatial location of vegetated areas (supply) and human settlements (demand) (Baró et al., 2017). Whereas the flow of some cultural services, such as outdoor recreation, depends mostly on human infrastructure connecting people to green spaces (Balmford et al., 2015; Schirpke et al., 2019b). To further explore variation in ES flow we must investigate how it is modulated by the landscape and understand which landscape attributes may facilitate or hinder ES flow depending on the ES and the spatial distribution of supply and demand areas.

As an example, pollination is modulated by the capacity of pollinators inhabiting natural/semi-natural habitats (supply) to move to pollination-dependent crops (demand) to perform the pollination service by visiting flowers (Brosi et al., 2008; Ferreira et al., 2015). In this case, a fragmented landscape may result in more contact (edge) between supply and demand areas facilitating the access of pollinators into crops to perform pollination (Fig. 2a). In less fragmented landscapes with large habitat patches adjacent to large homogeneous pollination-dependent crops, core crop areas may be more difficult to reach by pollinators due to isolation and possibly movement resistance imposed on pollinators by the crop matrix.

On the other hand, recreation services usually depend on people's mobility via any means of transportation, be it terrestrial, aerial, or waterway. As an illustration, consider a park with natural attractions such as an impressive waterfall (supply). Visitation of the waterfall will depend on people's willingness to visit this location (demand) and their ability to get there (i.e. the existence of roads, bus lines, bike paths or the proximity to a train station). In this example, ES flow occurs when people travel from their homes to the park. Distance from residence to the park may act as a limiting factor (Fig. 2b), which can be overcome by

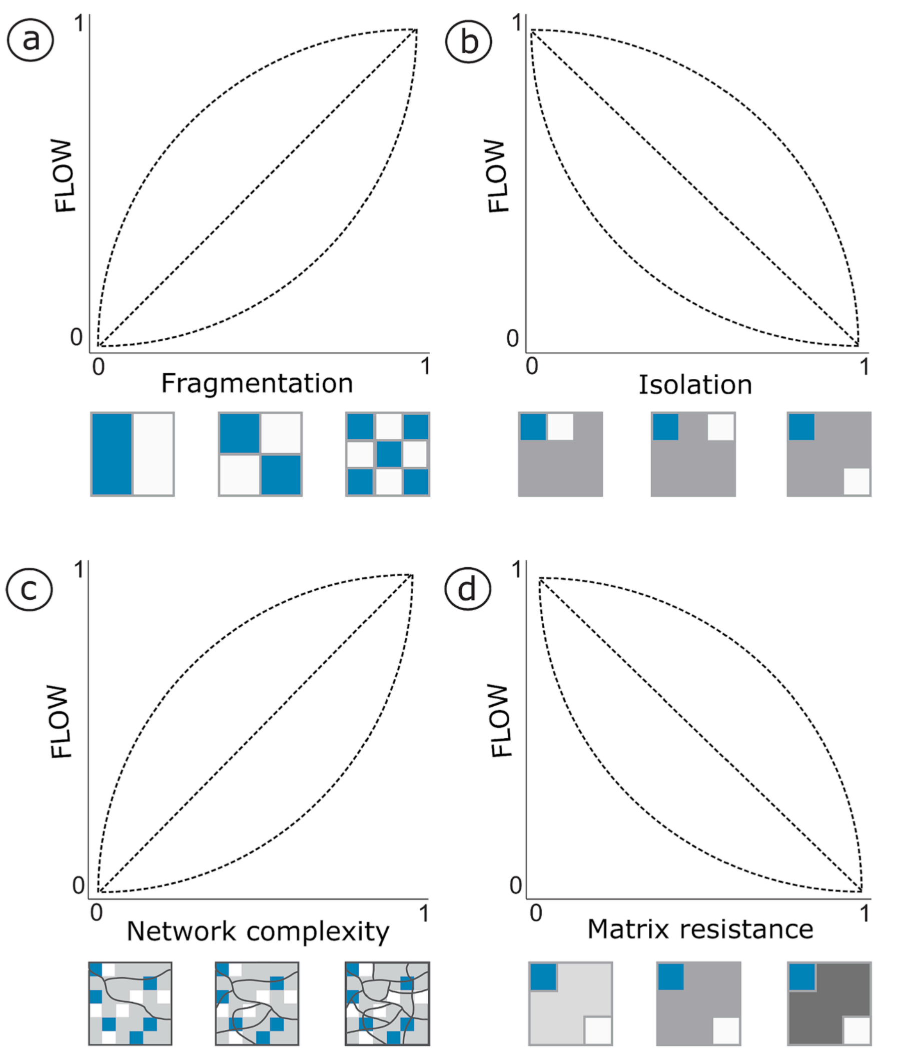

Fig. 2. Landscape management to optimize flow must rely on the effects of landscape configuration and composition on ES flow. We assume that certain landscape attributes will influence ES flow positively and others negatively, depending on the ES evaluated. However, we acknowledge that the actual variation in ES flow could be different than the hypothetical curves presented here. Squares represent landscapes with ecosystem service demand (white) and supply (blue) areas, and in some cases neutral areas (grey). Higher levels of fragmentation *per se* are expected to increase interspersion between supply and demand, facilitating flow to a certain degree for pollination (a). Increasing isolation between supply and demand areas will decrease flow of pest control (b). Complementarily, network complexity may facilitate flow not depending on distance, but on existing connections, as is the case of outdoor recreation (c). Likewise, matrix resistance may be limiting animal movement for pest control or other services dependent on that (d). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the existence of transportation infrastructure (Fig. 2c). However, the spatial arrangement of transportation infrastructure can be heterogeneous and focused on particular types of flow, for instance, connecting the park to nearby urban centers. In this case, it could be easier for people that live in the city to access the park instead of inhabitants of a closer nearby rural neighborhood, due to accessibility (Fig. 2c).

Moreover, timber, as a provisioning ES, depends on supply (e.g., forest type, tree stocks, tree age) and flow (e.g., logging techniques, transport capacity) to be delivered (Fig. 2c). In this example, demand for timber could be any factory or industry that uses timber as a raw material (Kastner et al., 2011). However, neutral areas in the landscape could restrict access to timber, depending on their characteristics (Fig. 2d). If a certain tree species was to be reached within a dense forest, relief, streams, and understory vegetation could be obstacles to reach and transport timber to nearby roads. On the other hand, the presence of a navigable river can facilitate access to certain remote areas.

Here we use these examples to illustrate how landscape configuration and the presence of certain elements within the landscape can facilitate or hinder ES flow depending on the mechanism and the arrangement of supply and demand in space. We acknowledge that the examples are not exhaustive and, thus, do not cover all possible variants. In summary, we expect that combined landscape characteristics will present different effects on the flow, and the complexity of landscape patterns (represented by a combination of metrics) must be explored in further research (see Duarte et al 2020).

3.2. How supply and demand ratios may affect ES flows

The arrangement of supply and demand areas determines the intensity of flow and whether maximum ES flow is attainable. Given a hypothetical landscape in which all the space is occupied by ES supply or demand areas (varying from being totally occupied by demand to totally occupied by supply), the maximum flow that could potentially occur of a non-rival ES (when the use by one does not prevent the use by another; see ES rivalry in Glossary) is not limited solely by the supply/demand ratio. In such cases, the spatial arrangement of supply and demand areas in the landscape may prevent the maximum flow occurring (Fig. 3), due to intrinsic characteristics of flow. Using microclimate regulation as an example of non-rival ES, consider an urban green space (ES supply) capable of reducing heat islands within 100-meter buffer area in a neighborhood. In this example, only if all demand is located within the 100-meter buffer, maximum flow will take place. Notice that in this case (and in others for which distance matters), the spatial distribution of supply can restrict the flow of the service depending on distance (Fig. 3a and b). In the case of microclimate regulation, flow will vary depending on the interspersion and size of green areas. The more interspersion

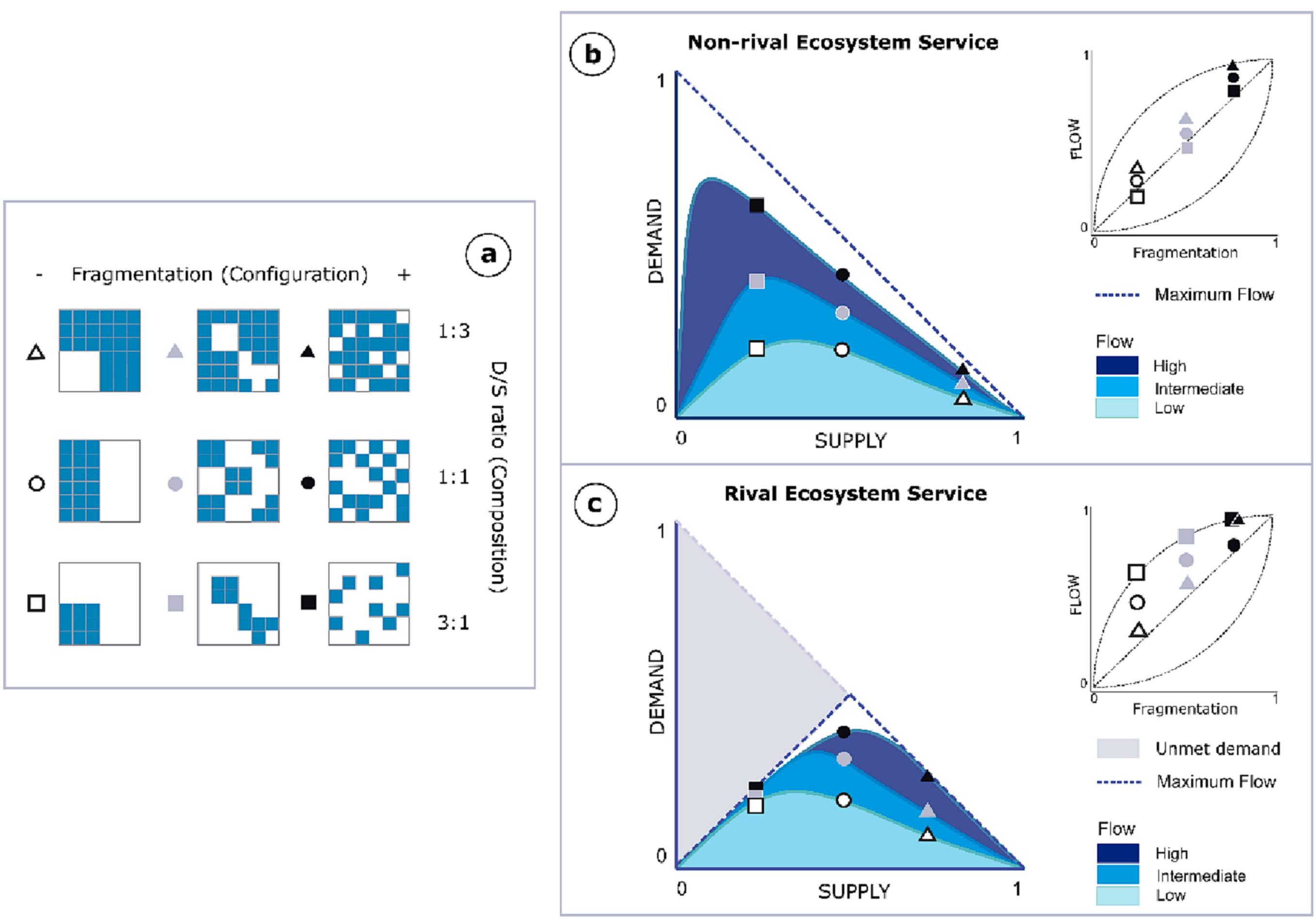

Fig. 3. Variation of flow along a demand/supply ratio (a) for non-rival (b) and rival (c) ecosystem services. Here we use a (a) variation in the degree of fragmentation between demand (white) and supply (blue) units to illustrate how it may affect flow (b and c). Maximum flow (dashed line) is limited by supply for rival ecosystem services (c). Blue shades illustrate flow variation under different landscape structures (b and c). White areas below dashed line (maximum flow) represent unmet demand when supply is available (b and c); grey area above dashed line represents unmet demand due to supply unavailability (c). Black, grey and unfilled symbols represent possible landscapes with a varying degree of fragmentation and D/S ratio. Examples of flow representation illustrate the difference between non-rival and rival ES: for the first, flow from the same supply unit may attend multiple demand units while for the second, flow from one supply unit to a demand unit prevents the flow to another demand unit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

among households and sidewalks the higher the flow of the service (black filled symbols in Fig. 3a and b). If all green space is concentrated in only one area or portion of the urban landscape, temperature will be lower in this area and its 100-meter surroundings but the rest of the neighborhood further away will not receive the flow (unfilled symbols in Fig. 3a and b).

On the other hand, the maximum flow of a rival ES is limited by supply/demand ratio (Fig. 3c). Using organic fruit produced in a community urban garden as an example of rival ES, the amount of supply will determine the demand that can be fulfilled. As demand for those organic fruits increases along with the number of people in the local community, the flow will be limited by the amount of fruit produced (Fig. 3c). People living further from the garden could have more limited access to the fruits, while people living adjacent to it could have more ready-to-go access. In this example, ES flow may be modulated by the distance between supply and demand and maybe the more centralized the garden is the higher the flow (grey and black filled circles in Fig. 3b and c), which might not be the case for other ES (see curves in flow versus fragmentation in 3b and 3c).

3.3. *Considering neutral areas in ES supply, demand, and flow*

In a real landscape, the existence of supply and demand areas is usually accompanied by the presence of neutral areas for a given ES (i.e. any land cover or land use that is not a supply or demand area for the specific ES; Fig. 4a). In such cases, the supply-demand ratio is affected by a decrease in demand areas (Fig. 4b), a decrease in supply areas (Fig. 4c), or both (Fig. 4d). Using pollination as an example of a regulating service, in a landscape with habitat remnants inhabited by pollinators (supply areas) and agricultural lands with a pollination-dependent crop (demand), the existence of pastures dominated by an exotic grass species could be considered a neutral area for the pollination service (Greenleaf et al., 2007; Ricketts, 2001). In this example, the amount (composition) and spatial arrangement (configuration) of landscape elements determine, in combination with pollinators' mobility and sensitivity to neutral areas, whether these can reach the crops and perform the service of pollination (i.e. ES flow).

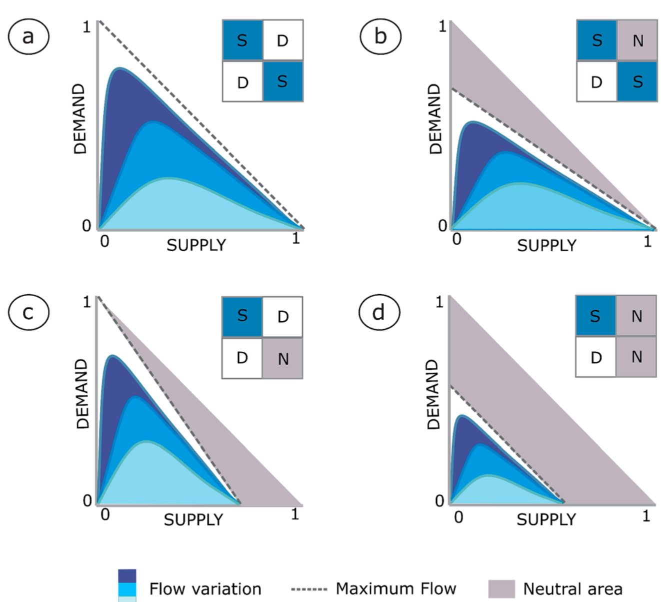

Fig. 4. Variation in the amount of neutral areas (N) will modify the maximum flow of ecosystem service (dashed lines) within a landscape. We exemplify flow shifts in a landscape with ecosystem service demand (D) and supply (S) areas in the absence of neutral areas (a); a landscape with neutral areas replacing and thus reducing demand areas (b); a landscape with neutral areas replacing and thus reducing supply areas (c); and finally, a landscape with neutral areas replacing and reducing both demand and supply areas (d).

If pastures were not present, the configuration of habitat and crops would modify ES flow, possibly more interspersed landscapes would have higher ES flow (darker blue in Fig. 4a) and less fragmented landscapes would have lower ES flow (lighter blue in Fig. 4a). In a landscape with neutral areas replacing demand areas (Fig. 4b), more habitat with some pasture and fewer crops, because the amount of crop (demand) is lower, maximum flow decreases accordingly (dashed line in Fig. 4b). If pastures exist spatially between habitat (e.g., native forest patches) and crops – and depending on crop extension – they may provide resistance to pollinator movement due to it being a matrix of high structural contrast and prevent them from reaching core crop areas, consequently lowering ES flow (lighter blue flow in Fig. 4b). On the other hand, when neutral areas substitute supply areas (Fig. 4c), less habitat can still be enough to enable maximum ES flow depending on the landscape configuration. Lower amounts of habitat can still allow high ES flow when there is a high amount of edge between habitat and crops (darker blue areas in Fig. 4c). However, if there is pasture in between them, again, ES flow will be reduced. Most certainly, landscapes with higher amounts of pastures would hinder pollinator movement from habitat to crops because the chance of pastures being present between them is higher (Fig. 4d). Nevertheless, ES flow would depend on the configuration of such elements. If instead of pastures, neutral areas were composed by a less resistant type of land use, for example a matrix of lower habitat-contrast such as eucalyptus plantation for forest dependent species, pollinator's mobility through these neutral areas could be higher, therefore providing higher ES flow, than a similar configuration with a more resistant neutral area (thus less permeable).

Using the microclimate regulation example, if there were empty lots (neutral areas) among the households in the neighborhood, that same amount of green space would be capable of supplying that same amount of service, however because demand is reduced, so is the maximum flow (dashed line in Fig. 4b). In this same example, if neutral areas replace supply (Fig. 4c) and demand remains the same, maximum flow can still be enough to fulfill demand. As such, the arrangement (i.e. landscape configuration) of households, green spaces and empty lots (demand, supply and neutral areas, respectively), and the S/D ratio, will determine ES flow (Fig. 4). Additionally, if instead of empty lots, neutral areas were composed by 5-floor buildings, spatial arrangement could hinder the temperature regulation, in case such constructions act as barriers for heat or limiting how far the cooling effect could reach.

3.4. *Spatial overlap can expand supply-demand ratios and ES flow*

In other cases, supply and demand areas may overlap or partially overlap (Fig. 5), depending on the scale of observation. For instance, regulating services promoted by mobile organisms, may have different supply and demand areas identified depending on the extent and resolution of the area being assessed. Less detailed maps may present bigger overlaps than more detailed ones. Whereas for other services, such as climate regulation, such variation in overlap might be not observed. Nonetheless, ES flow may still be affected by supply and demand spatial arrangement. As an example, the service of pest control depends on the existence of natural enemies that inhabit native habitat remnants (supply) and perform this regulation service in nearby crops (demand) (Boesing et al., 2017). In this case, ES flow would vary according to contact and distance between native habitat and crop (as the variation in the blue areas in Fig. 5a). Spatial overlap can be exemplified for the same service in agroforestry systems which can host pest controllers (supply) and at the same time can be the demand area for pest control (Fig. 5c; Perfecto et al., 2004). A combination of both cases, with habitat remnants, crop areas and agroforestry, represents a partial overlap (Fig. 5b). For biological pest control (Medeiros et al., 2019), the arrangement of supply and demand in space, as well as the overlap will determine the flow. The closer supply and demand are the higher the flow (Blanche et al., 2006). When overlapping, we expect the flow to be enhanced

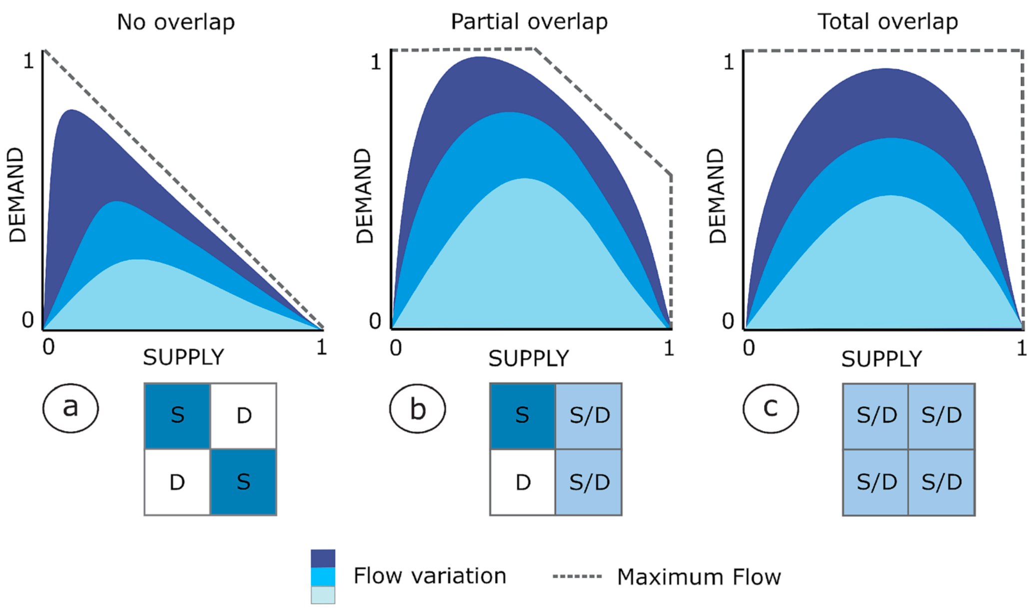

Fig. 5. Landscapes may contain spatial overlap between ecosystem service demand (D) and supply (S) areas. For landscapes in which there is no overlap, maximum flow of ecosystem services (dashed line) may occur between supply and demand areas (a). Flow can vary below maximum according to other landscape attributes (blue gradient). In some cases, there might be a partial overlap between supply and demand areas (b), or a more extreme total overlap may take place (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(compare blue flow variation and maximum flow areas in Fig. 5a with b and c). On the other hand, the less overlapped supply and demand are, the lower the flow between them (as in the light blue area in Fig. 5a).

4. Implications for the research agenda

Using landscape planning to optimize flow between supply and demand might be a feasible way to achieve more sustainable practices and long-term ES provision. If research efforts integrate all three components of the service provision chain (supply, flow, and demand) in ES assessments and improve the understanding on how landscape patterns influence each one of them, landscapes can be managed more efficiently to optimize flow, enhance supply, and regulate demand for ES. To advance and put our framework to practice, further research is needed to integrate this approach with other relevant aspects of the service supply chain. Here we highlight some challenges that must be overcome.

4.1. Quantifying supply and demand spatial variation

In our framework, we assume no variation in quality or amount of supply and demand per area unit. However, ecosystem conditions are heterogeneous and highly influenced by its surroundings, with important consequences for ES provision. Thus, when accounting for ES supply one must take the variation of ecosystem conditions into consideration. Likewise, ES demand per unit area depends on the actual demand of the persons which may vary according to their preferences and spatial unit used. Demand will vary depending on population density, consumption behavior, and culture (e.g. Washbourne et al., 2020), therefore its quantification and mapping should be further developed in collaboration between natural and social sciences. Besides, landscape structure may also affect demand due to how people experience and relate to a specific landscape. For example, Zoderer et al. (2019) found that farmers, rural inhabitants, and visitors of a given rural landscape may have distinct preferences for certain ES, therefore, influencing demand. Additionally, spatial characteristics of place of childhood and current residence also shape people's preferences and needs, which in turn can influence their demand for ES (Zoderer et al., 2019). Thus, our proposed framework can be tested not only by applying the existing knowledge of how environmental aspects shape the spatial distribution of supply and demand (e.g. nutrient regulation; Bicking et al., 2020), but also by combining it with new approaches to quantify ES demand based on stakeholder's perspectives (Zoderer et al., 2019; Washbourne et al., 2020).

4.2. Managing demand to enable optimal flow

Demand can be managed by the development of people's awareness about ES provision and therefore enabling their engagement in the development of policies to guarantee ES provision in the future (Metzger et al., 2021b). Demand management may become feasible with the recognition of societies' needs and priorities regarding ES provision (Peter et al., 2022). In our framework, consequences of the S/D ratio, their spatial organization, and the configuration of neutral elements will only be further elucidated once adequate assessments of demand can be performed. Further understanding the role of each component of the service provision chain and the landscape will enable them to be managed accordingly. However, for this purpose government, institutions and other interests must be aligned in the pursuit of collective well-being and sustainable practices. A few aspects to be considered, other than natural and social sciences joining efforts are a) how feasible it is to manage demand; b) how to improve methods to assess people's desires and needs; and c) how to value ecosystem services and benefits, not exclusively in monetary terms, so that governments can excel in serving citizens' needs, while institutions can seek more sustainable practices. Therefore, linking this to a landscape perspective is also necessary to elucidate how the fulfillment of local demand depends on local supply or on the supply of other landscapes (further regions; Schröter et al., 2018).

4.3. The role of co-production by humans on ES flow

Even though our framework does not explicitly consider the role of co-production by humans in determining ES flows, such inclusion in future assessments will help unravel new or additional patterns. Co-production processes can be a modifier of the spatial relationships for some ES. In section 3.1 we exemplified the role that infrastructure can play in increasing the access of humans to a specific location where they can benefit from a service, which could be considered a co-production component enhancing flow. However, a deeper understanding of how co-production pathways (Palomo et al., 2016) are related to spatial ES flows should facilitate its integration in ES assessments. It is likely that the spatial arrangement of supply and demand will be less important in those services (e.g. drinking water, food, recreational use) for which co-production plays a major role.

4.4. Exploring how neutral areas in the landscape affect ES flow

Neutral areas may be different for each ES, so we must consider this variation when dealing with multiple ES. Moreover, although not explored in-depth in our framework, neutral areas vary in how much resistance, therefore reduction, they can cause on flow, this is evident for ES that rely on the movement of organisms, but it can also be the case for ES mediated by air or water. For example, different agricultural areas (crops or pasture) can impose different movement resistance to birds (Barros et al., 2019; Boesing et al., 2017), thus the presence of a particular agricultural area between supply and demand areas can increase or decrease biological pest control services provided for demand areas by these natural enemies (Medeiros et al., 2019). Further elucidating the different roles of such neutral areas in the connection between supply and demand and the modulation of flow for different ES is the next step to be taken. For this, describing and clarifying flow mechanisms (e.g. those mediated by animal movement, people's movement, mass movement) and how they vary across neutral areas will guide the further comprehension of the role of anthropogenic matrix attributes (e.g., diversity, resistance, similarity, contact, distance).

4.5. Integrating temporal variation on S-D ratio assessments

Temporal variation in ecosystem conditions and consequently in ES supply brings consequences to flow and demand fulfillment. Nonetheless, demand also varies over time due to social aspects affecting people's desires and needs from nature. This perspective has gained attention in planning initiatives for sustainable futures since we need to account for variations in supply, flow, and demand through time for the long-term ES provision (Boesing et al., 2020). Fully considering this temporal variation is beyond the scope of this framework, but despite the very long way to go in the development of spatiotemporal approaches, scientists' awareness of such temporal variations may be the necessary heads up for management and policy development for the present time (Fremier et al., 2013). For example, an important aspect to be considered is how high demands and flow for certain ES may end up degrading supply (decreasing its quantity and quality), thus endangering long-term ES provision (Boesing et al., 2020). This is more straightforward for rival ES, but it may also occur for non-rival ES. For example, high visitation rates (flow) in protected areas can degrade hiking paths as well as the attractiveness of the place, thus degrading supply of the recreational service. Controlling the access of visitors (flow) may be enough to prevent degradation of supply and ensure the long-term flow of this service.

Another promising strategy is to include the temporal variation of ES provision into both the conservation and restoration agendas, because supply can be both protected, 'created' (i.e. restored, regenerated or recovered; Chazdon, 2008), or enhanced to assist unfulfilled demand. A possibility is to consider scenarios of future demand along with the capacity of ecosystems to provide benefits while making decisions regarding the management of protected areas. Similarly, research efforts could address whether there is a minimum amount of supply to guarantee long-term ES flow without affecting ES supply maintenance (Hein et al., 2016). Additionally, evaluating alternative scenarios with different spatial restoration options can optimize landscape structure that improves ES flow (Duarte et al., 2020). Time-lagged responses are to be expected when it comes to restoring ecosystems and their functions, therefore long-term spatial planning should anticipate the realization of ES flow and the long-term benefits of creating sustainable landscapes.

5. Conclusion

The flow of ES is fundamental to understand how spatial configuration can enhance or hinder ES provision. Here, we propose that spatial flows of ES are modulated not only by the amount of supply and demand, but by their spatial arrangement. We show that landscape configuration and the ratio of supply to demand will determine flow, including the maximum flow, depending on the type of ES (rival or non-rival). After careful consideration on the outcomes of changing the supply-demand ratio, we also acknowledge the crucial role played by 'in-between' areas (i.e. neutral areas), that despite not being supply or demand, can facilitate or hinder the spatial flows to occur. Several (and diverse) landscape processes are involved in the flow of each ES, and these are explored little in the literature. Thus, more attention should be given in future studies to the effects of the composition and configuration of neutral areas in the spatial flows of ES, and how such relationships would be affected by the S/D ratio and their spatial overlap. Overall, we reflect on the complex relationship between landscape structure and the service provision chain. There is a clear need to promote landscape approaches that address supply, flow and demand, their spatial configuration and composition (including neutral areas), in addition to accounting for ES rivalry on spatial flows. We expect our approach to be useful in advancing the knowledge necessary to overcome current landscape management limitations that fail to account for multiple ES and promote their long-term provision.

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

No data was used for the research described in the article.

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