Reframing landscape fragmentation's effects on ecosystem services

Matthew G.E. Mitchell[1], Andrés F. Suarez Castro[1], Maria Martinez-Harms[2], Martine Maron[1], Clive McAlpine[1], Kevin J. Gaston[3], Kasper Johansen[1], Jonathan Rhodes[1,2]

[1] School of Geography, Planning and Environmental Management, The University of Queensland, Brisbane, QLD 4072, Australia

[2] Australian Research Council Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, Brisbane, QLD 4072, Australia

[3] Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, United Kingdom

Abstract

Landscape structure and fragmentation have important effects on ecosystem services, with a common assumption that fragmentation reduces service provision. This is based on fragmentation's expected effects on ecosystem service supply, but ignores how fragmentation influences the flow of services to people. Here, we develop a new conceptual framework that explicitly considers the links between landscape fragmentation, the supply of services, and the flow of services to people. We argue that fragmentation's effects on ecosystem service flow can actually be positive or negative and use our framework to construct testable hypotheses about the effects of fragmentation on final ecosystem service provision. Empirical efforts to apply and test this framework are critical to improve landscape management for multiple ecosystem services.

Keywords: landscape fragmentation, ecosystem services, ecosystem service flow, ecosystem service supply, biodiversity

Landscape fragmentation: the need to reconceptualize for ecosystem services

Humans continue to heavily modify natural ecosystems around the world, with negative consequences for biodiversity (see Glossary) and natural capital [1,2]. At the same time, demand for ecosystems to provide benefits, or services, to society is growing rapidly [3]. This has significantly increased the need to understand and manage landscapes simultaneously for ecosystem services and biodiversity. Recently, the potential of managing landscape structure [4-6], and in particular landscape fragmentation [7,8], for these multiple goals has been highlighted. Interest in landscape fragmentation - the breaking apart of areas of natural land cover into smaller pieces independent of a change in the amount of natural land cover - has a long history in ecology [9]. Consequently, a well-developed understanding exists of its effects on biodiversity and ecosystem functioning [10]. However, the shift in research interest from biodiversity towards the concept of ecosystem services has recast what before were solely ecological questions into social-ecological ones [11-13]. This recasting means that predictions about the ecological effects of landscape fragmentation on biodiversity and ecosystem functioning are unlikely to translate directly into ecosystem service provision. This will be especially true if fragmentation has contrasting effects on people and how they interact with ecosystems to produce ecosystem services compared to biodiversity and ecosystem functioning. It is therefore critical to rethink how fragmentation alters all of the components of ecosystem service provision in order to improve landscape management for multiple services.

Ecosystem service provision depends on three elements: *supply*, *demand*, and *flow* (Figure 1), each of which can respond differently to landscape fragmentation. Ecosystem service supply is the potential for natural capital to generate a benefit for people, irrespective of it being realized or used [14]. In turn, ecosystem service demand is the level of service provision desired or required by people, and is influenced by human needs, values, cultures, institutions, and built capital [15]. Finally, for ecosystem service provision to be realized, people must interact with ecosystems to gain a benefit. This interaction connects service supply with demand to produce a service flow: the actual delivery of a service to people to be used or enjoyed [15].

Here, we argue that the effects of fragmentation on ecosystem service supply and flow can either complement or oppose each other, leading to contrasting net effects on service provision. Ecosystem service supply depends on the presence of particular species, ecosystems, or ecological processes that are often negatively affected by fragmentation. In contrast, most ecosystem service flows depend on the distribution and movement of organisms, matter, and people between areas of natural and anthropogenic land cover. For example, fragmentation of forests from logging, road construction, or agricultural and urban expansion can alter plant species composition and growth, negatively affecting water quality regulation and carbon sequestration [16,17]. At the same time, this fragmentation can improve forest access, increasing timber harvesting, hunting, wild food foraging, and park visits [18,19]. Thus, by altering the arrangement of areas of service supply and demand, or humans and natural capital across a landscape, fragmentation can modify ecosystem service supply, movements critical for service flow, and ultimately service provision.

That landscape fragmentation simultaneously affects ecosystem service supply and flow has not, thus far, been widely acknowledged in the development and application of the ecosystem service concept. The majority of ecosystem service studies that consider fragmentation focus only on service supply [4,20] and disregard demand and flow. Similarly, most ecosystem service decision-support and quantification tools focus on service supply and have limited ability to determine flow [21]. While tools such as InVEST (naturalcapitalproject.org/InVEST.html) and ARIES (ariesonline.org) aim to better quantify service flows across landscapes, integration of this information into decision-making remains limited and is still mainly focused on service supply. Consequently, predictions about how landscape fragmentation will affect ecosystem service provision are likely to be incorrect. This has important implications for landscape planning to optimize service provision.

To spur research in this area, we present a conceptual framework that links fragmentation explicitly with ecosystem service supply and flow, and use it to make testable predictions about the effects of landscape fragmentation on ecosystem service provision. We discuss how fragmentation could drive tradeoffs and synergies among services, highlighting the implications for policy and planning, and identify future research priorities for investigating the role of landscape fragmentation on ecosystem service provision.

Linking fragmentation to ecosystem service supply and flow

Here, we identify specific mechanisms by which landscape fragmentation, independent of the loss of natural land cover, affects service supply and flow (Figure 1), and the ultimate consequences of these relationships for service provision. A planning issue of critical importance in many human-dominated landscapes is how spatially to arrange areas of natural land cover within the human-dominated matrix [22,23]. While we recognize that alteration of the spatial arrangement of natural land cover also has important consequences for landscape heterogeneity, our framework simplifies this complexity by focusing on fragmentation of natural land cover. We feel this is a necessary first step to better develop a spatially explicit landscape-scale understanding of ecosystem services.

Fragmentation and ecosystem service supply

Fragmentation tends to drive biodiversity loss and shifts in ecosystem function [24,25], although a variety of responses can occur, especially at low or intermediate levels of fragmentation [9]. Fragmentation often reduces the ability of plant and animal species to move across landscapes, interrupting daily movements between foraging and breeding habitat, dispersal events, and migration [10]. In addition, smaller habitat patches support fewer species, contain smaller populations that are at greater risk of extinction [26], and have increased edge effects that can negatively affect the persistence of native species [27]. Each of these different effects of fragmentation can result in degradation of the natural capital and biodiversity that contribute to service supply (Figure 1).

There is widespread evidence that biodiversity influences or is strongly correlated with the supply of many ecosystem services [28,29]. For example, increased tree species richness [30] and plant diversity [6] are each associated with an increased supply of multiple ecosystem services. In particular, biodiversity is increasingly important as the number of services considered increases [31]. Thus, if biodiversity declines with landscape fragmentation, as is commonly observed [10], ecosystem service supply will also likely be lost.

Pollination and pest regulation are among the best-studied examples where landscape fragmentation drives this relationship. Increased species and functional diversity in pollinator or arthropod predator communities can increase service supply [32,33]. In turn, this diversity can be enhanced by increased forest and grassland connectivity or increased landscape complexity (smaller fields, more hedgerows) across agricultural landscapes [34,35]. Fragmentation can also affect forest plant diversity and the supply of carbon storage and sequestration [17,36], although this effect is not universal [37]. Similarly, fragmentation of marine ecosystems and rivers can have significant effects on aquatic biodiversity and fish abundance important for commercial fisheries [38,39]. Unfortunately, most of these examples only quantify service supply and not actual flows to people, which might be affected very differently by fragmentation.

Fragmentation and ecosystem service flow

For most ecosystem services, their flow depends on the movement of organisms, matter, energy, and/or people across landscapes to connect spatially separate locations of supply and demand (Figure 1)[20]. For example, pollination depends on the movement of native pollinators from fragments of non-crop vegetation into fields [40], drinking water provision relies on the flow of above- and below-ground water to areas of collection or consumption [41], and the movement of people to fishing locations or parks is needed for fisheries and recreation [42]. Conversely, some services depend on ecosystems restricting flows of organisms or matter. For example, flood regulation is provided when ecosystems restrict or delay water flow [43], disease regulation when the movements of disease vectors to people are limited [44], and water quality regulation when ecosystems capture or transform excess nutrients, sediments or pollutants [41].

Because ecosystem service flow relies on facilitating or restricting movement, landscape fragmentation can affect the magnitude and spatial pattern of these flows (Box 1)[20]. Importantly, fragmentation increases the interspersion of natural and anthropogenic lands, reducing distances between areas of service supply and demand, and potentially increasing service flow. At the same time, fragmentation affects the number, size, shape, spatial arrangement, and isolation of patches of natural land cover, which in turn can positively or negatively affect the flow of soil, water, energy, and organisms across landscapes [4]. Thus, fragmentation can have either negative or positive effects on service flow, depending on the service in question, the process of landscape fragmentation, and the resulting landscape structure (Box 1). In addition, the flow of some ecosystem services will be insensitive to fragmentation. For example, carbon sequestration and storage provides climate regulation globally regardless of its spatial location or the location of beneficiaries.

How fragmentation affects ecosystem service flow

Increased interspersion of natural and anthropogenic lands

Expansion of human land-use resulting in the fragmentation of natural land cover can place areas of service supply and demand in closer proximity to one another. For services that rely on the juxtaposition of ecosystems and people, this can increase service flows (Figure 2A). Services provided by mobile organisms often fall into this category. For example, interspersion of remnant forests and grasslands with cropland can maximize both pollination and pest regulation services [45]. Small reservoirs of regularly-placed natural land cover that provide shelter and nesting resources can more evenly distribute pollinators across agricultural landscapes and are predicted to maximize the flow of pollination services [22]. Similarly, regularly-spaced forest patch and hedgerow reservoirs of arthropod predators are needed to ensure an even flow of pest regulation to agricultural fields [46,47].

Increased fragmentation can also improve people's access to ecosystems to obtain recreational and health benefits. Increased visitation to parks and previously inaccessible wilderness areas when roads and trails are built can increase fishing, hunting, timber harvesting, and land clearing [18,19]. Similarly, in urban areas having nearby green spaces increases accessibility and can improve human health and well-being [48,49]. We predict that these effects of fragmentation on patterns of human movement, while often overlooked in the literature [4], will be as common and important for ecosystem service flow as those on the movement of other organisms.

Increased interspersion of people, their activities, and ecosystems can also increase flows of ecosystem disservices (damages or costs to people from ecosystems). For example, the spread of human diseases via biotic vectors is often greater when human habitation occurs in close proximity to natural areas. For Lyme's disease in North America, increased interspersion of people and forests is highly correlated with disease prevalence [50,51].

Increased isolation of patches of natural land cover

By isolating patches of natural land cover and reducing patch sizes, fragmentation can have negative effects on the movement of organisms and matter (Figure 2B). This is especially true if the intervening matrix impedes movement between patches. For services provided by mobile organisms [52], including pollination and seed dispersal, isolation can negatively affect service flow. For example, seed dispersal can be highly sensitive to forest fragmentation by agriculture, especially the loss of small forest patches that maintain landscape connectivity [53]. Services that rely on the movement of water can also be disproportionately affected. The presence of dams has fragmented most of Earths' major river systems, reducing water flow and the movement of people along these rivers, altering water provision to people, water quality regulation [54], and opportunities for recreation [55,56].

Decreased patch size and increased edge

Reduced patch size can decrease visitation rates and ecosystem service flows, for both organisms and people (Figure 2C). For example, smaller fields often experience less pollinator visitation compared to larger fields, with consequences for pollination and other services provided by mobile organisms [34,57]. Similarly, small parks attract fewer visitors from surrounding urban areas [58], reducing recreation [59] and other cultural services.

For those services that depend on restricting movement, increases in edge and edge:area ratio can have a variety of effects, either reducing or increasing service flow to people (Figure 2D). For example, fragmentation of areas of natural land cover by agriculture can result in greater vegetation-field edge and increased soil erosion [60,61] and nutrient loss [62,63], with consequences for downstream water quality. Contrastingly, linear patches of vegetation such as hedgerows can fragment the cropland matrix of agricultural landscapes, intercepting pesticides and odors and increasing air quality regulation [64,65]. Other directionally-provided ecosystem services, such as storm protection and flood regulation might also be improved by more linear wetlands [66].

Consequences for ecosystem service provision

The varied processes by which fragmentation affects landscape structure and heterogeneity, and thereby service flow, means that fragmentation's effects on supply and flow can be in parallel or opposition. We argue that this will result in a variety of landscape-scale fragmentation effects on the provision of different services, and hypothesize that three broad categories of effects are possible (Box 2). For example, when the effects of fragmentation on supply and flow oppose each other, service provision will peak at intermediate levels of fragmentation (Figure 3F). These three categories of relationships provide testable predictions of the effects of fragmentation on service provision.

The diverse effects of fragmentation on service provision will also drive positive and negative relationships between services in fragmented landscapes as each responds differently to the modified landscape structure, even if the services themselves do not interact strongly [67]. Importantly, our framework predicts that tradeoffs and synergies between ecosystem services might not always be unidirectional or constant, but could vary depending on the level of landscape fragmentation. Thus, we predict that managing landscape structure for ecosystem services does not simply involve minimizing fragmentation, but requires a much more complete understanding of the effects of landscape structure on service provision.

Challenges for ecosystem service science and policy

The challenge of incorporating the ecosystem services paradigm into environmental policy and landscape planning is increasingly being recognized [68,69]. The next major challenge is to develop a body of predictive theory to support policy and planning activities, similar to that currently present in biodiversity-fragmentation research. In this context, ecosystem service research needs to move away from simply quantifying and mapping the biophysical supply of services [70], and towards identifying locations of service demand, and potential pathways and magnitudes of service flow [15,20]. Understanding these different aspects of service provision and what features of landscape structure, fragmentation, and heterogeneity control them will significantly improve the ability to manage landscapes for ecosystem services. Our framework is a first step towards a more robust theory linking landscape structure with ecosystem services.

We propose that ecosystem service supply will decline with increasing fragmentation, but that the flow of ecosystem services to beneficiaries can increase or decrease. Thus, fragmentation of the landscape can either enhance or degrade ecosystem service provision (Box 2). We also argue that the responses of ecosystem service flow to fragmentation are driven by: (a) increased interspersion of anthropogenic and natural lands, (b) increased isolation of patches of natural land cover, and (c) reduced patch sizes and increased amounts of edge. These predictions reflect a number of important gaps in current knowledge and highlight a number of key research questions that will best address them (Box 3). In particular, testing our hypotheses across landscape gradients of fragmentation by quantifying the supply, demand, and flow of multiple services is an essential next step. Only in this way will the mechanisms by which fragmentation drives both service provision and tradeoffs between services be identified. Describing the precise form of the relationships between fragmentation and service provision, and identifying if distinct classes of relationships exist, similar to those in our framework, are also critical questions for future research.

Landscape planning almost always involves decisions about the spatial arrangement of conflicting land-uses that influence the level of landscape fragmentation (e.g. [71]). Active urban and rural landscape planning could benefit substantially from a more nuanced understanding of the relationships between landscape fragmentation and heterogeneity, and ecosystem service provision. Yet implications for other globally relevant policy challenges are equally important. Understanding when and why fragmentation inhibits or enhances ecosystem service provision is central to the land sparing versus land sharing (or wildlife-friendly farming) debate [23,72]. This is also true for designing rules to improve the effectiveness and co-benefits from trades in carbon markets (e.g. REDD+)[73], biodiversity (e.g. offsetting, agri-environment schemes) [5,74], and other ecosystem services (e.g. water quality). Market-based approaches to stimulate desirable land-use outcomes are also increasingly incorporating effects of spatial configuration [75], but currently incorporate only a simple understanding of the consequences of fragmentation. Thus, understanding the effects of fragmentation on ecosystem services is of critical importance for developing effective policy mechanisms.

Concluding Remarks

Our conceptual framework highlights the vital importance of understanding how fragmentation of natural land cover affects service supply and flow and the different ecological and social components of ecosystem service provision. Incorporating these effects into ecosystem service assessments is critical to develop effective tools that can help structure landscapes to provide multiple ecosystem services. In many ways, the field of ecosystem services is ideally placed to address this challenge; many studies already work at large spatial scales across landscapes with different levels of fragmentation, and incorporate data from a diversity of sources, including ecological, remote sensing, and social survey data. What is needed now is increased empirical research into the exact nature of the relationships between fragmentation and ecosystem service supply and flow. As the ecosystem services concept is increasingly incorporated into decision-making and planning activities, the need to improve understanding of ecosystem service provision at the landscape-scale is fundamentally important.

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Figure 1. A conceptual diagram of the effects of landscape fragmentation on the provision of ecosystem services. Fragmentation alters ecosystem service supply by affecting natural capital. This occurs when fragmentation affects the movement and distribution of organisms, matter, and energy across a landscape, with consequences for the biodiversity and ecosystem functions that are important for service provision. Fragmentation also affects patterns of human distribution, activities, and movement across the landscape. Combined, these effects influence the magnitude and spatial pattern of ecosystem service flows that connect areas of service supply to areas of demand. Thus, ecosystem service flows, and ultimately service provision, depend on how landscape fragmentation and the resulting landscape structure affect the movement and distribution of both ecosystems and people. In turn, the benefit derived from an ecosystem service affects service demand by altering human wellbeing and needs. This demand then drives human activities that alter landscape fragmentation (*dashed arrow*). Ecosystem service provision can also directly affect natural capital (*dashed arrow*) through over-exploitation. Adapted from [14].

Box 1. What is landscape fragmentation and how does it affect ecosystem service flow?

Landscape fragmentation is the breaking up of larger areas of natural land cover into smaller, more isolated patches, independent of a change in the total area of natural land cover (Figure 2). Landscape fragmentation causes three main interconnected changes to patches of natural land cover across a landscape: (i) an increase in the isolation of patches and their interspersion with the surrounding human-dominated land (e.g., agricultural or urban areas), (ii) an increase in the number of patches and the amount of patch edge, and (iii) a decrease in average patch area [9]. Simultaneously, the surrounding human-dominated portion of the landscape can become more connected as fragmentation proceeds, with important consequences for the movement and abundance of species that inhabit this portion of the landscape [52,76].

Thus, landscape fragmentation results in a number of interrelated effects for landscape structure, including changes to landscape configuration and heterogeneity. This means that a variety of mechanisms and effects on ecosystem service flow are possible (Figure 2). Fragmentation affects ecosystem service flows by facilitating or interrupting movement of organisms, matter, energy, and people across landscapes. This includes the daily movements of mobile organisms like pollinators and insect predators across agricultural landscapes; long-distance migrations; directional overland flows of water and the nutrients, pollutants, and eroded soil it contains; ocean and atmospheric currents at multiple spatial scales; and the movement of people across landscapes. The final effect of fragmentation on service provision will depend heavily on these processes and the key species, ecosystem functions, biophysical flows, and human activities that underlie each service, as well as the exact form and amount of landscape fragmentation that takes place. Additionally, the scale at which fragmentation takes place relative to ecosystem service flow will also change how it affects service provision.

Figure 2. The mechanisms by which landscape fragmentation, independent of a change in the area of natural land cover, can affect ecosystem service flow. Locations of natural land cover and ecosystem service supply (*green* areas)

provide ecosystem service flows (*red* arrows) and benefits (*red* areas) to the human-dominated matrix (*light brown* areas) that are affected by landscape fragmentation. Ecosystem service flows of organisms and people (*arrows*) can depend on proximity to natural areas (**A**) and will therefore be influenced by the interspersion of natural and anthropogenic land cover across the landscape (e.g., recreation, pollination, waste treatment, pest regulation). At the same time, increased isolation of patches and reduced connectivity (**B**), as well as decreased patch size (**C**), can decrease service flow in fragmented landscapes (e.g., pollination, seed dispersal, cultural services, watercourse recreation, water provision and regulation). Finally, for services that depend on restricting movement across landscapes, increased edge amounts with fragmentation (**D**) can have positive (e.g., storm protection, air quality regulation) or negative (e.g., water quality or soil erosion regulation) effects on ecosystem service flow. In each panel, the area of natural land cover and ecosystem service supply is unchanged between intact and fragmented landscapes. Adapted from [66].

Box 2. Combining the effects of fragmentation on ecosystem service supply and flow

Our conceptual framework predicts that a range of relationships between landscape fragmentation and final ecosystem service provision are possible depending on the specific processes by which fragmentation affects service supply and flow (Figure 3). While a range of effects is likely, we identify three general categories of effects:

(1) *Double Whammy*: fragmentation negatively affects both supply and flow, resulting most often in rapid and dramatic decreases in ecosystem service

provision with fragmentation. We predict this relationship for services where reduced connectivity and decreased patch size drive reductions in service flow (e.g., water provision and regulation, watercourse recreation, and pollination and pest regulation at high levels of landscape fragmentation).

(2) *Compensating*: the effects of fragmentation on flow oppose those on supply, resulting in increased service provision at intermediate levels of fragmentation. The exact level of fragmentation that maximizes service provision depends on the strength and shape of the relationship between fragmentation and service flow. Services where interspersion of natural land cover and human-dominated areas determines service flow should respond in this way (e.g., recreation, cultural and aesthetic services, genetic resources, pollination, and pest regulation)

(3) *Supply Driven*: ecosystem service flows are insensitive to fragmentation, therefore final service provision is simply a function of the effects of fragmentation on service supply. Examples include carbon sequestration, carbon storage, and the existence value of biodiversity.

Because there is a wide range of possible patterns of ecosystem service provision with fragmentation, this will drive synergies and tradeoffs between services in fragmented landscapes. For example, services that respond in 'Double Whammy' or 'Supply Driven' ways to fragmentation might show positive relationships across landscapes as fragmentation varies. Of course, variation in the strength of these relationships will also occur (e.g., *blue* versus *red* lines in Figure 3E). Contrastingly, tradeoffs might occur among services following a 'Compensating' relationship. Here, the strength of the trade-offs between services will depend on the level of fragmentation and resulting landscape structure. Tradeoffs and synergies between services and switches between the two could also occur within the 'Compensating' category as levels of fragmentation vary (e.g., *green dashed* versus *blue solid* line in Figure 3F). Thus, our framework predicts that tradeoffs and synergies between services might not always be unidirectional or constant, but will vary depending on the level of landscape fragmentation.

Figure 3. Effects of landscape fragmentation on the supply and the flow of ecosystem services will affect the final relationship between landscape fragmentation and ecosystem service provision. Landscape fragmentation, by reducing biodiversity and ecosystem function, is (**A**) predicted to reduce ecosystem service supply (three alternative possible trajectories are shown: *red*, *green*, and *blue* lines). At the same time, the amount of flow per unit of ecosystem service supply to beneficiaries can also be affected (**B**) negatively, (**C**) positively, or (**D**) be insensitive to landscape fragmentation (e.g., carbon sequestration), with a range of relationships possible (e.g., *solid, dashed,* and *dotted lines*). Combining ecosystem service supply and flow multiplicatively (**E**,**F**,**G**) will result in distinct relationships between landscape fragmentation and ecosystem service provision. Each of the trend lines in (**E**,**F**,**G**) is a combination of the lines in the plots above. Note that some lines overlap in (**E**) and for clarity not all possible combinations of supply and flow are shown; the *grey* lines in (**E**) show what provision would be if flow was insensitive to fragmentation.

Box 3. Outstanding questions about the effects of fragmentation on ecosystem services

(1) What are the specific relationships between landscape fragmentation and ecosystem service supply and flow for different services? While there is likely wide variation in the form of these relationships, this has yet to be quantified. This is a key first step to creating landscape management tools for ecosystem services that deal with fragmentation.

(2) What are the important mechanisms by which fragmentation affects service flow for different ecosystem services, and do these vary depending on spatial scale considered? We identify four potential mechanisms, but their relative importance across different services is largely unknown. Understanding these mechanisms is key to creating a predictive framework for the effects of landscape fragmentation on ecosystem service provision.

(3) Can the relationships between fragmentation and ecosystem service flow and final provision be generalized for specific categories of services? While we identify three broad potential categories (Figure 3), there might be additional categories or there might be instances where relationships between services and fragmentation are idiosyncratic depending on the scale of fragmentation or other biophysical and social factors. While we hypothesize that this is unlikely, it has yet to be tested.

(4) How are positive or negative relationships between ecosystem services affected by landscape fragmentation? Our framework predicts that these relationships might not be constant, but could vary across gradients of fragmentation or landscape structure. The prevalence and actual form of these relationships need to be tested in real landscapes.

(5) How can the effects of fragmentation on ecosystem service provision be effectively integrated into decision-making? The causes of fragmentation across landscapes are varied and it can often be driven by external factors such as demand for ecosystem services from distant locations. Therefore, effectively integrating knowledge about the effects of fragmentation into landscape planning will likely be difficult and effective paths to do this are yet to be explored.

(6) What is the most important component of ecosystem service provision (i.e., supply or flow) to understand with respect to landscape planning? With limited resources available to investigate how fragmentation affects both service supply and flow, determining which is most important for landscape management is critical to efficient decision-making.

Glossary

Benefit: the ways in which ecosystems improve human wellbeing via the provision of ecosystem services. Constituents of human wellbeing include materials essential for life, and contributions to health, security, social relations, and freedom of choice and action [77].

Biodiversity: the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. Defined here following the 1993 Convention on Biological Diversity (CBD) meaning of 'biological diversity', which we assume is equivalent to 'biodiversity' (www.cbd.int/convention/articles).

Connectivity: the degree to which a landscape facilitates the movement of organisms and matter [78]. We use the term to include both biotic connectivity (movement of organisms) and abiotic connectivity (movement of water, nutrients, and soil) across landscapes.

Ecosystem function: the flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem that allow or could allow natural systems to provide ecosystem services [79].

Ecosystem service: defined broadly, the biophysical and social conditions and processes by which people, directly or indirectly, obtain benefits from ecosystems that sustain and fulfill human life [77].

Ecosystem service demand: the level of service provision desired or required by people. Demand is influenced by human needs, values, institutions, built capital, and technology [15].

Ecosystem service flow: the actual delivery to or realization of an ecosystem service by people. Ecosystem service flow depends on both the supply of and demand for a service [14,15] as well as the movement of organisms, matter, and people [4].

Ecosystem service supply: the full potential of ecological functions or biophysical elements in an ecosystem to provide a given ecosystem service, without consideration of whether humans recognize, use, or value that function or element [14,15].

Landscape: a heterogeneous area composed of interacting ecosystems that is repeated in similar form throughout, including both natural and anthropogenic land covers, across which humans interact with their environment [80].

Landscape fragmentation: the breaking apart of areas of natural land cover into several smaller areas within a human-dominated matrix, without any change in the area of natural land cover [9].

Landscape heterogeneity: the amount of variation in landscape structure (composition and configuration) at a particular spatial scale across a landscape. Landscape heterogeneity is affected by landscape fragmentation through changes to patterns of spatial complexity.

Landscape structure: the arrangement of land covers and land uses across a landscape. Broadly, it includes landscape composition (how much of each land cover or land use that exists), configuration (the spatial pattern of these land cover or land use types), and connectivity.

Landscape matrix: the surrounding portion of the landscape in which fragments of natural land cover are located. In most cases we consider the matrix to be the human-dominated or disturbed areas of the landscape (e.g., agricultural fields, urban areas, cleared land). Characteristics of the matrix can be important for determining landscape connectivity and ecosystem service flow.

Natural capital: the stock of natural ecosystems, including all of their biological and physical features that supply flows of ecosystem services to people.

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Figure 1

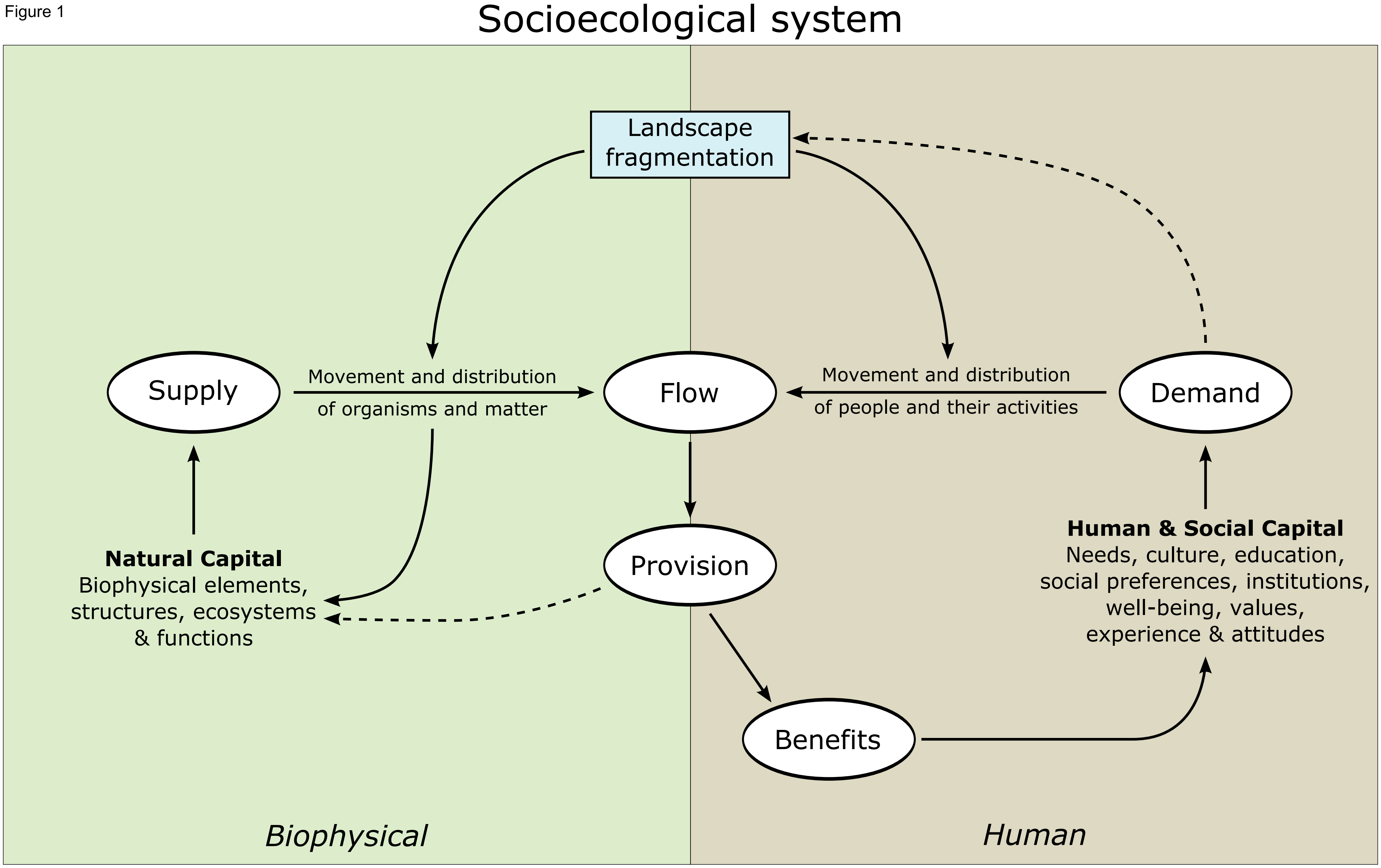

Socioecological system
Landscape fragmentation
Supply
Movement and distribution
of organisms and matter
Flow
Movement and distribution
of people and their activities
Demand
Provision
Natural Capital
Biophysical elements,
structures, ecosystems
& functions
Human & Social Capital
Needs, culture, education,
social preferences, institutions,
well-being, values,
experience & attitudes
Benefits
Biophysical
Human

Figure 2

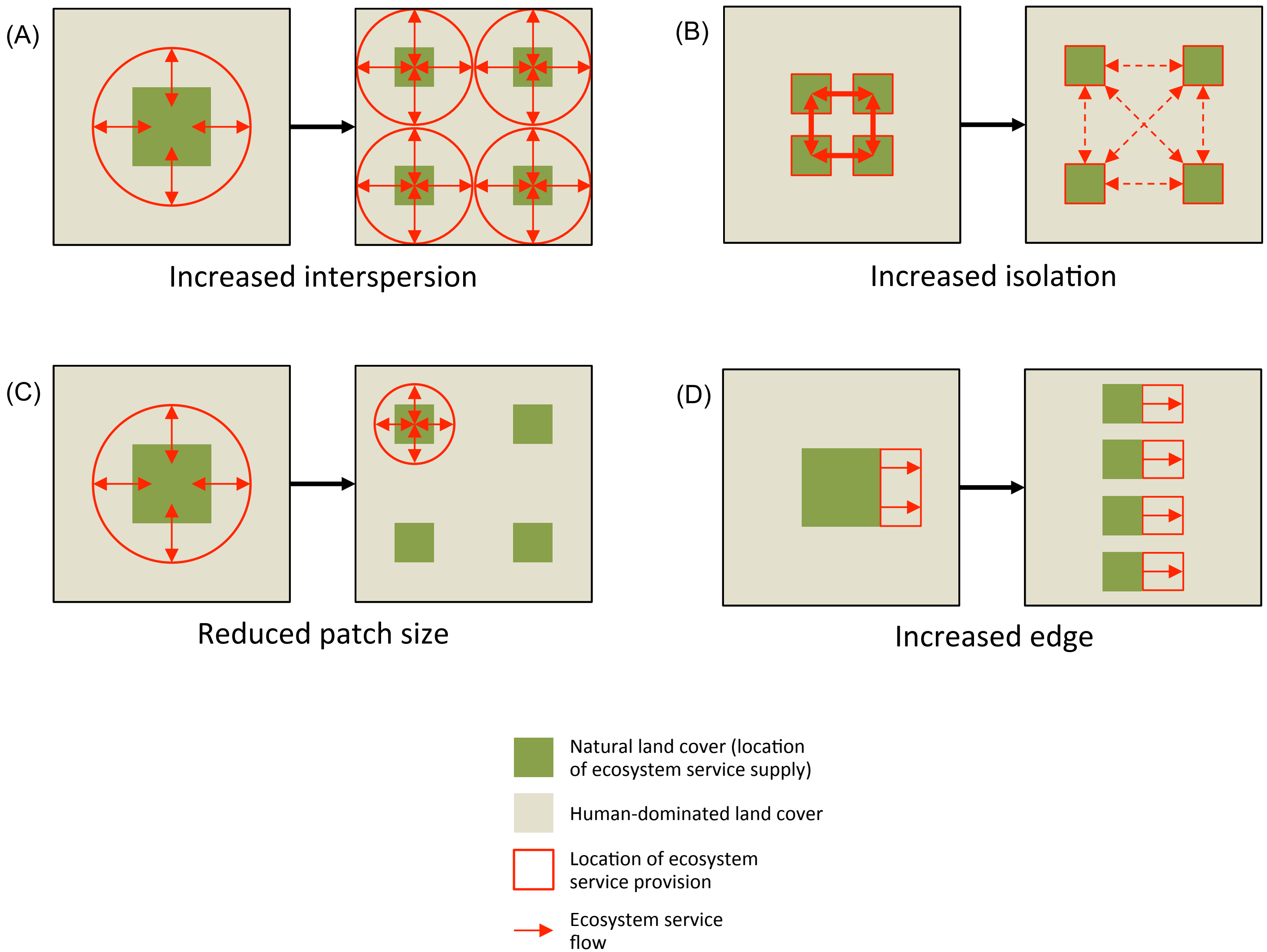
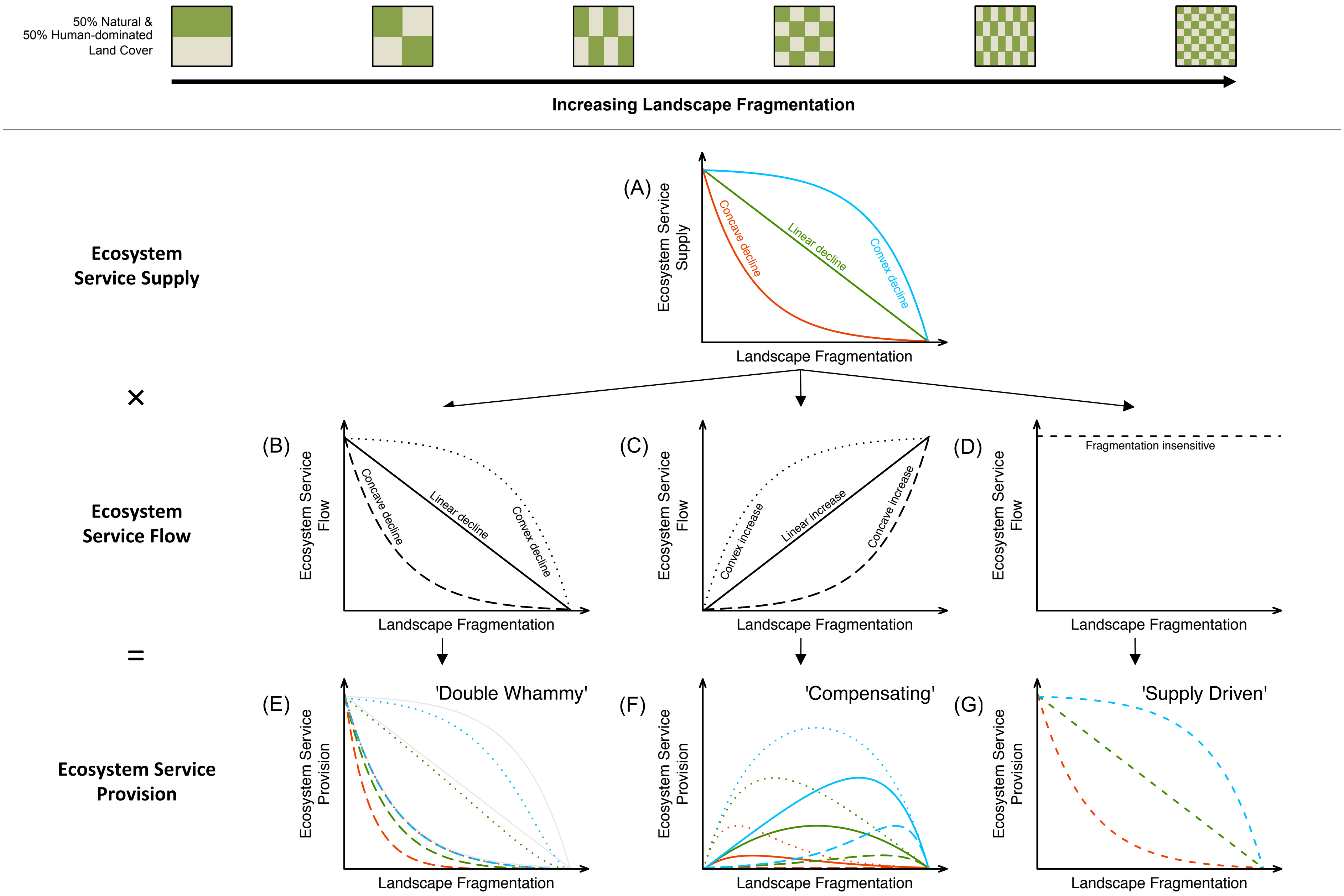

(A)
Increased interspersion
(B)
Increased isolation
(C)
Reduced patch size
(D)
Increased edge
Natural land cover (location of ecosystem service supply)
Human-dominated land cover
Location of ecosystem service provision
Ecosystem service flow

Figure 3



50% Natural &
50% Human-dominated
Land Cover
Increasing Landscape Fragmentation
Ecosystem Service Supply
×
Ecosystem Service Flow
=
Ecosystem Service Provision
(A)
Ecosystem Service Supply
Concave decline
Linear decline
Convex decline
Landscape Fragmentation
(B)
Ecosystem Service Flow
Concave decline
Linear decline
Convex decline
Landscape Fragmentation
(C)
Ecosystem Service Flow
Convex increase
Linear increase
Concave increase
Landscape Fragmentation
(D)
Ecosystem Service Flow
Fragmentation insensitive
Landscape Fragmentation
(E)
'Double Whammy'
Ecosystem Service Provision
Landscape Fragmentation
(F)
'Compensating'
Ecosystem Service Provision
Landscape Fragmentation
(G)
'Supply Driven'
Ecosystem Service Provision
Landscape Fragmentation