Opinion

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Reframing landscape fragmentation's effects on ecosystem services

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Landscape structure and fragmentation have important effects on ecosystem services, with a common assumption being 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 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 improving landscape management for multiple ecosystem services.

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 toward the concept of ecosystem services has recast what before were solely ecological questions into social–ecological

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Glossary

Benefit: the ways in which ecosystems improve human well-being via the provision of ecosystem services. Constituents of human well-being include materials essential for life and contributions to health, security, social relations, and freedom of choice and action [76].
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 to be equivalent to 'biodiversity' (http://www.cbd.int/convention/articles).
Connectivity: the degree to which a landscape facilitates the movement of organisms and matter [77]. 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 allows or could allow natural systems to provide ecosystem services [78].
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 [76].
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 delivery of an ecosystem service to people or its realization. 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 comprising interacting ecosystems that are repeated in similar form throughout, including both natural and anthropogenic land cover, across which humans interact with their environment [79].
Landscape fragmentation: the breaking apart of areas of natural land cover into several smaller areas within a human-dominated matrix, independent of 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 matrix: the portion of the landscape that surrounds fragments of natural land cover. 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.
Landscape structure: the arrangement of land cover and land use 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.
Natural capital: the stock of natural ecosystems, including all of their biological and physical features that supply flows of ecosystem services to people.

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 with 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 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]. Simultaneously, 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. Most ecosystem service studies that consider fragmentation focus on service supply only [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 (http://naturalcapitalproject.org/InVEST.html) and ARIES (http://ariesonline.org) aim to better quantify service flows across landscapes, integration of this information into

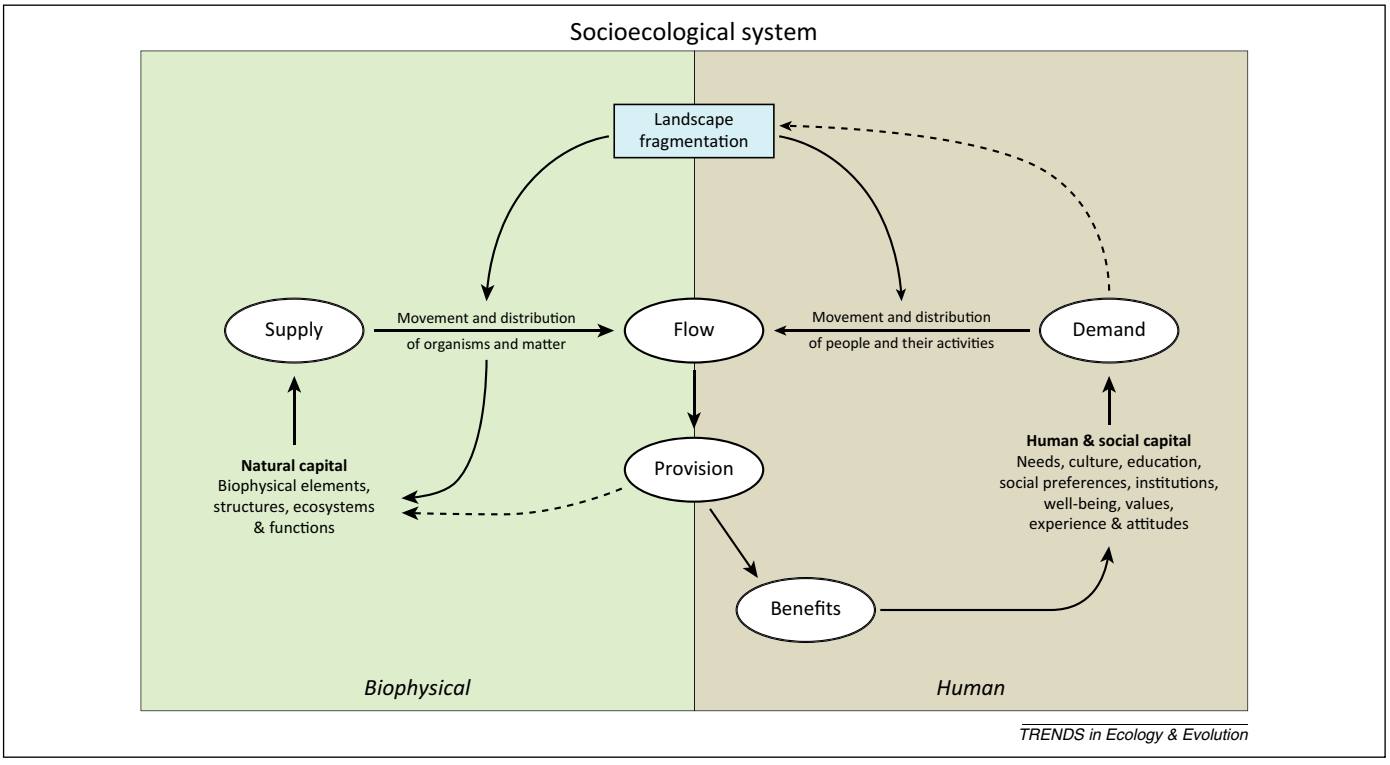

Figure 1. A conceptual diagram of the effects of landscape fragmentation on the provision of ecosystem services. Fragmentation alters ecosystem service supply by affecting natural capital. This occurs when fragmentation affects the movement and distribution of organisms, matter, and energy across a landscape, 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 well-being and needs. This demand then drives human activities that alter landscape fragmentation (broken arrow). Ecosystem service provision can also directly affect natural capital (broken arrow) through overexploitation. Adapted from [14].