



Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks

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Abstract

Characteristics of streams and rivers reflect variations in local geomorphology, climate, natural disturbance regimes and the dynamic features of the riparian forest. Hierarchical interactions between these components result in a rich variety of distinct stream communities which, when considered in combination with strong biotic feedbacks to the physical environment, present formidable challenges in discovering and understanding fundamental, system-level characteristics of natural rivers. The objectives of this article are to briefly review the traditional view of hierarchical physical controls on stream structure and dynamics and to show how this viewpoint is changing as recognition of strong biological influences on physical structure are emerging. In combination, identifying natural stream characteristics and the interactions among individual components, as well as recognizing the importance of biotic feedbacks on physical structure, form the basis for establishing effective conservation strategies.

Introduction

Much like other terrestrial and aquatic systems, flowing waters are structured and influenced by various biophysical agents. Variations in local geomorphology, climate, natural disturbance regimes and riparian corridor dynamics are all reflected within specific characteristics of lotic ecosystems. Interactions between these various biophysical components result in a continuum of in-stream conditions. These interactions, when coupled with the many human uses of the landscape, present formidable challenges in themselves for discovering and understanding fundamental, system-level characteristics of streams and rivers.

In essence, the key elements regulating watershed vitality in the temperate regions of North America and Europe are the delivery and routing of water, sediment, chemicals (ions and nutrients) and organic material to rivers; the temperature regime; and the characteristics of the riparian forest. These environmental features, in combination with the spatial position of a stream reach within the larger drainage network, are traditionally thought to exert hierarchical controls on the biotic character of stream ecosystems (Figure 1). However,

recent research suggests that there are strong feedbacks from the biotic components that also act to shape the physical environment.

The purpose of this article is to briefly review some of the more traditional viewpoints on physical control of the biotic community and then to discuss some of the more recent advances in river and stream ecology addressing biotic feedbacks shaping the character of the physical system. Some of these advances may be 'discoveries' in a more pure, scientific sense, while others may simply represent new perspectives in how one views the flowing water ecosystems of the world.

Traditional viewpoints on physical controls

It is widely recognized that there are strong and continuous interactions between geomorphology, hydrology, water chemistry and temperature. For example, consideration of both geomorphology and hydrology is still central in the debate about an acceptable worldwide classification of rivers (Rosgen, 1994; Miller & Ritter, 1996), while hydrology and temperature are linked in their effects on the life histories of many

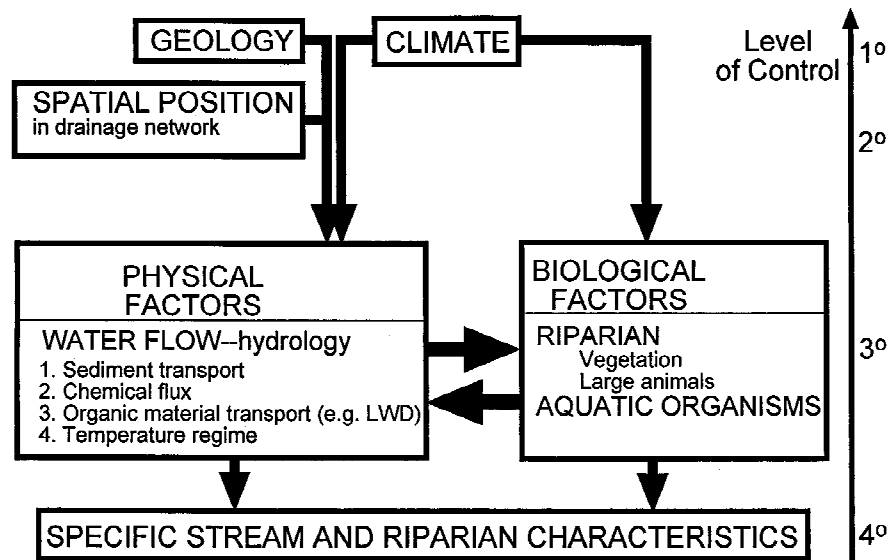


Figure 1. Shown is the concept of hierarchical controls over stream ecosystems, specifically the relative strength of factors (denoted by the width of the arrows) influencing stream characteristics, as well as some principal feed-back loops between components (from Naiman et al., 1992). Traditionally, components have been ranked hierarchically to show dominance of one component over another. However, it is now known that there may be strong feedbacks from lower components to ones that are ranked higher.

aquatic organisms (Ward, 1989). Here we provide a brief overview of each topic, setting the stage for a discussion of biotic feedbacks.

Channel geomorphology

Physical characteristics and processes related to landforms are of primary importance in understanding the structure and dynamics of lotic ecosystems. This fact ultimately provided the basis for the River Continuum Concept (Vannote et al., 1980) and related perspectives (Naiman et al., 1988a). Geologic landforms typically reflect:

1. interactions among tectonic processes that govern the development of topographic relief,
2. processes of erosion,
3. structure and lithology of the substrate, and
4. influences of climate (Montgomery, 1997).

Geomorphic processes in riverine corridors typically are affected by the type, frequency and intensity of natural disturbance. Disturbance characteristics typically reflect the spatial position of channel segments within the drainage network, and geomorphic processes (e.g. material delivery, routing and deposition) are highly interactive with hydrologic patterns and riparian vegetation, acting to shape the biotic characteristics (Naiman et al., 1992).

Hydrologic patterns

Streamflow can be considered a 'master variable' shaping in-stream conditions, given that it is correlated with many physicochemical variables, including water temperature, water quality, channel geomorphology and habitat diversity (Resh et al., 1988; Power et al., 1995). Lotic flow regimes show regional patterns that are determined primarily by river size and by geographic heterogeneity in climate, geology, topography and vegetative cover.

Poff et al. (1997) characterized five critical components of streamflow regimes that regulate ecological processes: magnitude, frequency, duration, timing and rate of change (i.e. flashiness). The *magnitude* of discharge refers simply to the amount of water moving past a fixed location in a given unit of time. The *frequency* of occurrence refers to the relative frequency of a streamflow event of a given magnitude (i.e. the concept of a 50- or 100-year flood). The *duration* refers to the period of time associated with a specific flow condition. The *timing* of a flow of a given magnitude refers to the regularity of occurrence (i.e. its *predictability*). Annual peak flows, for instance, may occur with low or high seasonal predictability. The *rate of change* or *flashiness* refers to how quickly flow changes from one condition to another.

These flow-regime components all vary within and

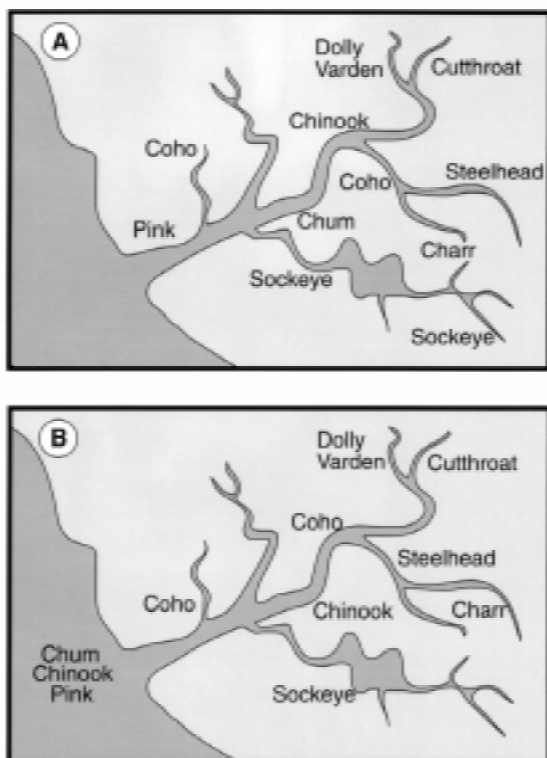


Figure 2. Shown are the relative positions in which selected salmonid species typically (a) spawn and (b) rear. Note that chinook (*Oncorhynchus tshawytscha*) are shown in two different rearing positions; this species exhibits two distinct life history strategies, one in which fry rear in the stream, and another in which emerging fry immediately migrate to sea and rear in saltwater.

between watersheds in an array of spatial and temporal patterns. A mosaic of habitat types result from these hydrologic variations; a single river may provide ephemeral, seasonal and persistent habitat patches which range from free-flowing, to standing, to no water. And for many lotic species, completion of the life cycle requires an array of habitat types, whose availability over time is regulated by the natural flow regime (e.g. Reeves et al., 1996; Naiman & Anderson, 1997). Consider, for instance, salmonids, which often require different habitat across life history stages (Figure 2). Salmonid species vary in their need for spawning habitat; different species ultimately utilize different spatial positions within the watershed. Coastal cutthroat trout (*Oncorhynchus clarki*) generally prefer cool, heavily-shaded headwater reaches, while chum salmon (*O. keta*) typically spawn lower in the watershed, often within the main channel. Rearing habitat is often different from spawning locales, and it, too, typically varies between species. Coho sal-

mon (*O. kisutch*) normally spawn in the main channel, while emerging fry may move into off-channel habitats to feed and rear. Natural flow regime dynamics are largely responsible for the creation and maintenance of areas like off-channel rearing areas. Migratory access to these areas is subject to the timing of inundation, and many fish species have adapted to the temporal phases of off-channel access. The flow regime regulates the degree of lateral connectivity a given lotic system experiences.

The magnitude and frequency of flow extremes regulate numerous ecological processes; they in fact create 'bottlenecks' which present critical stresses and opportunities for a wide array of riverine species (Poff & Ward, 1989). Organic detritus and attached algae are transported by flow, and periods of high flow remove and transport fine sediments that clog the interstitial spaces in otherwise productive gravel habitats (Beschta & Jackson, 1979). Floods also regulate other vital riverine processes, such as the delivery of LWD, the establishment of disturbance-adapted riparian species, and the development of aquatic habitat in the floodplain. The timing of flood events are also of critical importance to many aquatic and riparian species; life history events such as egg hatching, spawning and migration are often highly flow-dependent (Ward, 1989; Naiman & Anderson, 1997).

Chemistry and temperature

Dissolved nutrients and ions have a large influence on the kinds, amounts and activities of organisms present in streams. Inorganic ion and nutrient concentrations often reflect the erodeability and solubility of the underlying geology, whereas the type and concentrations of organic materials often reflect watershed vegetation, soil processes, water residence time on the land and in the drainage network, and the ability of microbes to decompose specific materials (Welch et al., 1998).

Water temperatures and the type and duration of ice cover also have strong controls on the biotic community. Water temperatures control and synchronize most physiological functions of ectothermic life forms (Ward, 1989; Naiman & Anderson, 1997). Temperature is a crucial determinant of the incubation rate of eggs and influences the growth rates of all aquatic organisms. Where seasonal water temperatures are extreme, patchiness in temperature throughout the drainage network becomes important in the persistence of some species as well as in maintaining a diversity of life history strategies in the same species.

Ice poses special challenges for aquatic organisms (Prowse & Gridley, 1993). Each of the basic types of ice – surface ice, anchor ice and frazil ice (i.e. ice particles which may be present in the flowing water column) – has different consequences for the organisms. Anchor ice is probably the most disruptive to bottom-dwelling organisms because of its tendency to exclude organisms from the sediments and to raft sediments if the ice mass is large enough to float. Rivers with substantial ice formation each year tend to be dominated by low-diversity communities and contain numerous insect species that complete their life cycles in less than one year. In contrast, rivers with less regular ice formation tend to have higher diversity and to contain insect species that may take several years to complete their life cycles.

The importance of biotic feedbacks

Characteristics of the riparian corridor

The riparian perspective toward river ecology is of a relatively recent genesis, especially when compared with other advances in limnology (Hynes, 1975; Naiman & Décamps, 1990, 1997). Clearly, there are strong effects of hydrology and landform on the development of riparian forests, and these have been well-documented (Gregory et al., 1991), as have the influences of the riparian forest on the trophic character of streams (via the type and amount of allochthonous inputs; Fisher & Likens, 1973) and on water quality (Haycock et al., 1996). Although the notion that riparian forests shape the physical structure of the lotic system (although recognized some time ago by geomorphologists; Keller & Swanson, 1979), it has been only recently quantified ecologically in terms of the spatial and temporal dynamics of large woody debris (LWD).

LWD in the many of the stream ecosystems of North America is a primary determinant of channel morphology where it forms pools, regulates transport of sediment and particulate organic matter, and provides habitat and cover for fish and other biota (Bilby & Bisson, 1998). Deposited LWD often forms a low gradient area upstream of the debris jam, providing a locale for sediment and organic matter deposition. In some instances, LWD may initiate the formation of islands where vegetation colonization, growth and island coalescence is realized (Fetherston et al., 1995). Streams that have seen significant anthropogenic disturbance in the riparian zone often suffer from

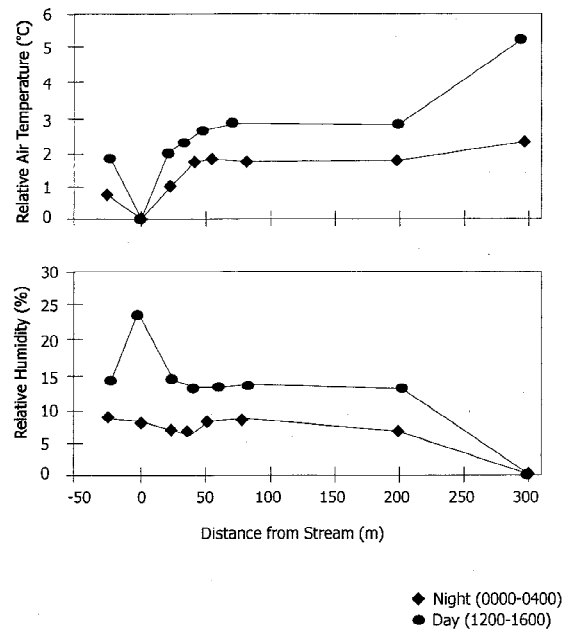


Figure 3. Shown are microclimatic data for riparian forests in western Washington. Both relative humidity and air temperature are influenced by the stream for distances of 31–62m away from the channel (adapted from Broszofski et al., 1997).

a lack of LWD recruitment, as well as LWD being cleared from channels (Piégay & Gurnell, 1997). The replacement of riparian forests by early-successional, easily-decayed litter may result in a long-term degradation of the quantity and quality of deposited LWD, ultimately compromising factors such as the proportion of retained organic matter and a decline in habitat value for aquatic organisms (Ralph et al., 1994). LWD in tropical regions, however, appears to play a lesser role in shaping the physical environment due to the widespread distribution of termites (Naiman & Rogers, 1997).

LWD decay rates are of interest in some ecosystems where debris may last an especially long time. Surface LWD on the Queets River, Washington (U.S.A.), has been dated to over 1500 years before present (ybp; most dates are <300 ybp, T. Hyatt & R. J. Naiman, unpublished data), while a stream in western Tasmania has significant surface LWD which dates 2000 to 4000 ybp (Nanson et al., 1995). Not only do the riparian forests and associated LWD shape the function and structure of forested streams, often LWD continues to influence the physical character of the streams for centuries to millennia.

Microclimate gradients

The notion that the riparian forest influences stream temperatures via shading of solar radiation has been known for some time (Beschta et al., 1987). Brosf-ske et al. (1997) have shown that small streams (2–4 m width) and their riparian zones modify air temperature and humidity for distances ranging from 31–62 m away from the channel in temperate rain forest streams (Figure 3). These results are especially important for resource management since more conservative riparian buffer widths of 10–25 m may not be adequate for preserving an unaltered microclimate or adequate growing conditions for a typical vegetative community.

In addition, the role of riparian vegetation in retaining water and attenuating the downstream effects of floods is an important landscape-scale function (Décamps, 1996). Water retention by plants and LWD in the riparian zone increases local relative humidity affecting the pattern and diversity of the vegetative community (Pollock et al., 1998).

The effects of large animals

Historically, animals have been viewed as passive components of ecosystems, responding merely to the conditions to which they are subjected. In many cases, however, large animals are responsible for biogeochemical, successional and landscape alterations that may persist for centuries (Naiman, 1988; Butler, 1995).

Early accounts of North American and European landscapes indicated a seemingly unlimited supply of migratory birds, fishes, fur-bearing mammals and large assemblages of mammalian herbivores. Some early North American accounts documented the strong interactions between these animals and the ecosystems supporting them (e.g. Bartram, 1791; Morgan, 1868; Hays, 1871). The extirpation of a number of these megafauna have eliminated their functional role from selected ecosystems, but evidence of the long-term effects of animal influences still remains (e.g. mima mounds, beaver meadows). In addition to this, a number of large animals, such as beaver (*Castor canadensis*) are now recolonizing much of their former range (due to factors such as the relative lack of predators, laws regulating take and increasing forage and habitat) and once again demonstrating some influences on the physical characteristics of streams.

Riverine systems are among the ecosystems in which animal influences have played a dominant role,

although their role largely has been omitted from discussions of biophysical influences on flowing waters. This omission is particularly unfortunate, given that their influence is second only to the aforementioned primary physical factors (Naiman & Rogers, 1997). Large animals in riverine ecosystems can significantly alter both the structure (channel geomorphology, vegetative characteristics, biodiversity) and function (productivity, connectivity, resistance and resilience to disturbance) of river corridors (Figure 4).

Many ecologists and resource managers have maintained a single-species approach to the analysis of animal impacts on rivers and streams. Typically, aquatic mammal species (e.g. beaver) and riparian browsers (e.g. moose, *Alces alces*, or elk, *Cervus canadensis*) have been studied and managed separately. This focus has failed to recognize the synergistic forces that result from the interactions among riverine megafauna; indeed community interactions among species have long-term, complex ecosystem-level consequences (Butler, 1995; Naiman & Rogers, 1997). A striking example of how large animals modify the physical environment is provided by beaver. Through the cutting of wood and the construction of dams, beaver retain sediments and organic matter, create and maintain wetlands, modify nutrient cycling and decomposition dynamics, modify riparian structure and dynamics, influence the character of materials transported downstream, and ultimately influence plant and animal community composition and diversity (e.g. Naiman & Melillo, 1984). With regard to the latter point, the activities of beaver have been shown to replace invertebrate taxa normally adapted to running-waters with pond taxa (McDowell & Naiman, 1986), generate a striking increase in the biomass of lotic invertebrates per unit area (Naiman et al., 1986), and influence fish assemblages (Snodgrass & Meffe, 1998).

Interactions between species are of particular importance in influencing the physical structure of riverine ecosystems. Many Pacific species of anadromous salmon and trout (*Oncorhynchus* spp.) are semelparous (i.e. they die after spawning) and their carcasses represent a significant seasonal nutrient contribution to the system in which they perish. Epilithic organic matter, many aquatic macroinvertebrates and rearing salmonids have all been shown to be enriched with marine-derived nitrogen (¹⁵N) in systems supporting anadromous salmonids (Bilby et al., 1996; Larkin & Slaney, 1997). Riparian vegetation adjacent to these streams are also ¹⁵N enriched, indicating

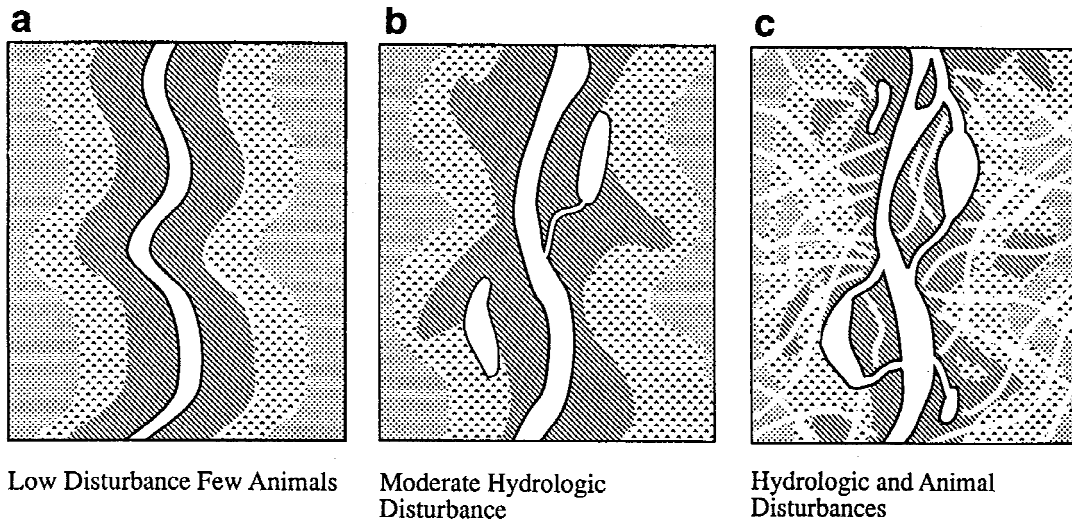


Figure 4. When channel processes are constrained by management, the result is a vegetation mosaic in a simple linear form (a). Under the influence of natural hydrologic and channel processes, heterogeneity is improved (b). Patch heterogeneity is optimized, however, only with the feeding and movements of large animals. Patches are smaller, more numerous, and more spatially dispersed under the influence of large animals (from Naiman & Rogers, 1997).

that vectors (such as grizzly bear, *Ursus arctos*) may be important in distributing limiting nutrients within the system (J. Helfield & R. J. Naiman, unpublished data). Given that most temperate ecosystems are N-limited, this contribution of marine-derived nutrients, including the distribution by various vectors, is a significant process for both the riparian vegetation (which produces LWD) and for in-channel production.

In river corridors, numbers of animals and abundance (and quality) of food also vary constantly, and the variations are irregular in time, space and ecological amplitude. These variations are interconnected; variations in animal abundance indirectly effect the abundance of others, and may indirectly affect the trophic dynamic of the system in question. Selective foraging by some large mammals (e.g. moose, *Alces alces*) can change ecosystem properties such as plant species composition, nutrient cycling rates and soil fertility. For example, selective browsing by moose on hardwood species allows unbrowsed or lightly browsed conifers to dominate the boreal landscape (McInnes et al., 1992); increasing relative abundance of conifer litter may depress the availability of soil N, often the limiting nutrient in boreal forest ecosystem productivity. Foraging strategies of individual moose may result in the creation of riparian and terrestrial landscapes which strongly affect both the vegetation (browse density and distribution) and, in turn, moose population density and survival (Moen et al., 1998).

Synthesis

The traditional view of top-down, hierarchical control of stream environments by geomorphic and hydrologic regimes remains valid. The purpose of this article is not to challenge this widely accepted and robust concept but to show that the concept, to be fully descriptive, requires modification to include biotic influences on the physical components as well. Geomorphic and hydrologic processes continue to provide strong influences on the physical template of streams and continue to form the basis for the development and maintenance of biotic communities and processes. Nevertheless, recent advances in stream ecology have demonstrated that certain biotic components also exhibit strong influences on geomorphology, hydrology and microclimate, helping shape the physical environment.

Human intervention can seriously disrupt important natural feedbacks between the biotic and physical environments. By altering natural flow regimes, modifying the riparian corridor, and directly and indirectly introducing or removing various plant and animal species, human beings have significantly altered the majority of the world's riverine ecosystems. For example, LWD deposition, forest establishment, and subsequent LWD deposition represents a process 'loop' vital to the long-term integrity of a natural stream system. Riparian modifications that result from forest manage-

ment alter the LWD cycle, disrupting vital feedbacks to the physical environment (Naiman et al., 1992, 1997; Ralph et al., 1994). Replacement of mature riparian forests with stands dominated by early successional species alters the quality and quantity of recruitable LWD. Many early successional species are smaller (and therefore less likely to remain within the system through a flood season) and decay faster than late-successional species. Invasive plant species can have long-term effects on the geomorphology of channels, as seen in the Platte (Johnson, 1994), Colorado and Green (Graf, 1978) rivers in the United States. The net consequence is that long-term system-level modifications result from direct or indirect modifications to the riparian forest or to other sources of channel-shaping LWD.

Likewise, many large animal species that exert considerable influences on the structure and function of rivers and streams have been significantly affected by man's activities. Migrating salmon and trout are important components of many coastal systems, for example, yet suffer from the effects of various land use practices as well as from near-sighted fishery resource exploitation. The long-term effects of eliminating the seasonal 'pulse' of marine-derived nutrients in naturally oligotrophic coastal streams and rivers are not known precisely but are suspected to be significant. In addition, the extirpation of beaver from much of their former range (as well as their recolonization of this habitat) fundamentally altered the character of streams throughout the upper third of the world (Naiman et al., 1988b, 1994).

The perspective addressed in this article, that specific biotic components have strong feedbacks to the physical system, is not new. However, as new data are generated and new viewpoints toward streams are explored, biotic feedbacks appear to be more prevalent than originally expected. Indeed, there are strong long-term linkages between the physical and biological components and those linkages have influences and strengths in both directions, possibly with equal intensity.

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