Moreover, there are limitations to our current understanding of evolutionary mechanisms. In particular, even if one subscribes wholeheartedly to the adaptationist program, one cannot ignore the fact that evolution is also highly *contingent*: evolution works in a blindly local sense with the materials at hand (Dawkins, 1987), constrained by a phylogenetic history that itself recursively reflects the past contingency of evolutionary dynamics (for different perspectives on evolutionary contingency, see, e.g., Ulanowicz, 1986; Kauffman, 1993; Brown, 1994b). If particular species play a dominant role in some ecosystem function, the vagaries of dispersal histories will usually restrict these species (except *Homo sapiens*, alas) to particular geographical regions. This introduces a substantial historical contingency into ecosystem processes.

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Shachak, M. and C. G. Jones. 1995: Ecological flow chains and ecological systems: concepts for linking species and ecosystem perspectives. Pages 280-294 *in* C. G. Jones and John H. Lawton, editors. Linking Species & Ecosystems. Chapman and Hall, New York.

A deep the
future will require recognition that both species and ecosystems have histories, and that these histories reflect a mixture of predictable results from general laws, and the idiosyncratic results of accidents—evolutionary contingencies. It is this blend of order and chance that makes the study of life such an endlessly satisfying endeavor. In this noble enterprise, evolutionary biology and ecosystem science should be mutually reinforcing partners.

ACKNOWLEDGMENTS

I would like to thank Bob Sterner and Mike Vanni for an invigorating conversation held at 9,000 ft. in the Rockies, and an anonymous reviewer for helpful (even if annoying) comments.

27

ECOLOGICAL FLOW CHAINS AND ECOLOGICAL SYSTEMS: CONCEPTS FOR LINKING SPECIES AND ECOSYSTEM PERSPECTIVES

Moshe Shachak and Clive G. Jones

SUMMARY

One way to link population/community ecology with ecosystem ecology is to interconnect flows of organismal abundance with flows of materials. Using an example of isopod population dynamics, soil erosion, and hydrology in the Negev Desert, Israel, we show how disparate flows of different currencies can be functionally connected. We use two concepts, Ecological Flow Chains and Ecological Systems, to generate a question-driven, multiflow, multicurrency, multiscalar representation of relationships among isopod, soil, and water flows. We provide general definitions and criteria for these two concepts, so that they can be used inductively or deductively to link many different flows of nature.

UNDERSTANDING THE FLOWS OF NATURE

All ecological processes are spatially and temporally dynamic and can be thought of as flows of different currencies (e.g., solar energy, nitrogen, genes, organismal density, species diversity). Tansley's (1935) "basic units of nature" contain many flows that interact (e.g., materials that affect organismal abundance and vice versa). Some ecologists focus on a particular flow of a particular currency (e.g., information, organisms, energy, materials, or structure). This "uniflow–unicurrency" approach leads to detailed understanding of a particular flow that can be readily measured in nature, but tells us little about how flows interact. Other ecologists focus on entire ecosystems (i.e., networks of flows) using a single, universal currency (see Brown, Ch. 2) such as information, materials, or energy (see DeAngelis, Ch. 25). This "multiflow–unicurrency" approach leads to general understanding of the entire ecosystem at the expense of detailed information about particular flows that can be readily measured in nature.

In order to link population/community ecology with ecosystem ecology we need to combine the advantages of both "uniflow–unicurrency" and "multiflow–unicurrency" approaches retaining detailed information about specific, measurable flows of different currencies (e.g., population dynamics vs. materials cycles) while also tractably linking many flows of different currencies (e.g., population dynamics with material flows). Our approach uses two general concepts—Ecological Flow Chains and Ecological Systems—to generate question-driven representations of nature that have multiflow, multicurrency, and multiscalar properties. Here, we use an example from the Negev Desert, Israel to show how functional interrelationships among a flow of organisms and flows of materials can be inductively described, explained, and scaled using ecological flow chains (EFCs) that are connected to produce an ecological system (ES). We then develop formal definitions of EFCs and ESs, and briefly outline the principles for inductively and deductively applying these concepts.

INDUCTIVE UNDERSTANDING OF SOME FLOWS OF NATURE: AN EXAMPLE

Relationships Among Isopods, Water, and Soil

Studies in the Negev Desert Highlands, Israel (1972–1993) had the goal of understanding interactions among desert isopod population dynamics and hydrology and soil processes. *Hemilepistus reamuri*, the desert isopod, is a detritivorous arthropod with an annual life cycle (Shachak et al., 1979; Linsenmair, 1984). Isopods live as a monogamous family of parents and offspring in a single soil burrow (Shachak, 1980; Linsenmair, 1984). In February, adult isopods (2 cm long, 200 mg FW) leave the burrow in which they hatched and developed, seeking new sites in which to settle (Shachak and Brand, 1991). Isopods emigrate distances of up to 1 km (Shachak and Newton, 1985). About 10% of the emigrating females are successful in locating a new site for a burrow (Shachak and Yair, 1984). Females select a new site in a patch of soil, digging a shallow burrow (ca. 5 cm depth) and accepting a male after a brief courtship (Shachak et al., 1976). Females are gravid by April, and 80–120 offspring hatch in May (Shachak and Newton, 1985; Shachak and Brand, 1988). Parents and young live in the burrow until the following year, communally digging down to the relatively high soil moisture (ca. 6–10% by weight) that persists throughout the 7-month dry season (May–November) at depths of 50–70 cm (Yair and Shachak, 1982, 1987). Only those families that dug burrows at sites with high soil moisture content survive (about 50% of the families of settling females, i.e., 5% of the total emigrating females) (Shachak and Brand, 1988).

The moisture regimen in a small patch of soil (ca. 50 cm diameter) is determined by the amount of rainfall falling on the patch and infiltrating the soil *and* the amount of runoff water entering and infiltrating the same soil patch (Karnieli, 1982). Average annual rainfall during the 5-month wet season (December–April) in this region of the Negev is 90 mm with high interannual variance (CV 40%) (Sharon, 1980). Direct precipitation within a year is usually insufficient to generate the high soil moisture levels required by isopods (Karnieli, 1982). However, this limestone desert highland (200–450 m above sea level) has watersheds (0.02–0.2 km^2) with rock slabs at the top, rocks with soil patches in the midslope, and mostly soil at the bottom. Runoff water from the adjacent upslope rocks that then infiltrates the soil patches is the critical, major source of soil moisture (Yair, 1985). The ratio of local rock area to soil area determines the amount of runoff. At low rock-to-soil ratios (< 0.2) soil moisture content immediately following a high rainfall event (ca. 25 mm) is low (ca. 20% by weight) because water primarily comes from direct rainfall. At high rock-to-soil ratios (1–5) soil moisture content from the same rain event is much higher (up to 37% by weight), with the runoff contributing as much as two to three times more water to a soil patch than direct rainfall (Yair and Danin, 1980; Olsvig-Whittaker et al., 1983). Soil moisture from runoff can persist in the soil for up to 3 years, and the accumulation and persistence of soil moisture from rain (persists for up to 1 year) and runoff are critical in determining isopod settling and establishment (Shachak and Yair, 1984).

The rock-to-soil ratio at a given locale changes over time and is largely determined by local soil erosion (Yair and Shachak, 1987). Undisturbed surface soil is relatively nonerodible because it is colonized by a microphytic crust (cyanobacteria, algae, mosses, and lichens) (Evenari et al., 1982). Isopods are engineers (sensu Lawton and Jones, Ch. 14; Jones et al., 1994). During feeding and burrowing they consume large quantities of soil. The fecal pellets, which look like tiny bricks (3 mm^3), are composed almost entirely of soil particles. Feces are removed from the burrow every morning and are deposited in a circle around the burrow entrance. By October the large pile of feces (ca. 250 g per burrow representing an excavated volume of ca. 250–350 cm^3) shows that a family has successfully survived (Shachak and Brand, 1988). The accumulation of fecal pellets on the soil surface is the major source of erodible soil in a soil patch. During 1973–1990 erodible soil production by *H. reamuri* on a rocky slope in the Negev averaged 170 ± 109 kg ha^{-1} year^{-1}, which represented about 60% of the total erodible soil production in the watershed (Yair and Shachak, 1987).

The fecal pellets on the soil surface are eroded by overland runoff that occurs when runoff exceeds soil infiltration capacity during periodic rainfall events of higher magnitude (Yair and Shachak, 1987). These runoff events occur about 10 times per year on average in the wet season (max. 23 events), and carry the soil from areas with a high rock-to-soil ratio to areas with a low rock-to-soil ratio, that is, from the upper slope to the midslope and from the midslope to the wadi. Runoff is the most important factor determining soil erosion at these scales (Yair et al., 1978). The feces discarded by the isopods are readily disintegrated under the direct impact of raindrops and runoff, and the resulting erodible soil particles are transported by the overland flow of runoff water (Yair et al., 1978).

Isopod formation of erodible soil plays a major role in determining the local rock-to-soil ratio by facilitating soil erosion. By increasing or maintaining a high rock-to-soil ratio the isopods increase the relative contribution of runoff as a soil moisture source, increasing soil moisture content. Because soil moisture content determines site suitability for isopods and isopod density, there is a feedback to isopods and their soil engineering activities. Ecological questions about a particular flow, that is, isopod population dynamics or water or soil flows, or about the interrelationships between population dynamics and material fluxes, can both be addressed from a functional understanding of these interconnections.

Representing and Connecting the Flows of Isopods, Water, and Soil

We can treat isopod population dynamics, hydrology, and soil erosion as flows. Each flow can be represented by an Ecological Flow Chain (EFC) (Fig. 27-1). Each flow chain functionally *describes* the flow of one of the three currencies of interest as a connected series of *organizational state changes*. The Isopod Flow Chain (IFC) consists of changes in abundance of potential settlers to settlers and settlers to successful families. Changes from organizational state to organizational state (i.e., potential settlers to settlers, settlers to successful families) describe the flow of isopod numbers, that is, their population dynamics. The Water Flow Chain (WFC) consists of changes in the amount of rainfall to runoff, rainfall to soil moisture, and runoff to soil moisture that describe this particular hydrologic flow. The Soil Flow Chain (SFC) consists of changes in the amount of nonerodible soil to erodible soil and erodible soil to eroded soil that describe this particular soil flow. Each of these EFCs has dynamic behavior (i.e., changes in the organizational states) that are, in part, intrinsic to the flow chain. Thus changes in the number of potential settlers influences the number of settlers which, in turn, influences the number of successful families; erodible soil is formed from nonerodible soil and is necessary for soil erosion; rain is necessary for runoff to occur; and both rain and runoff determine soil moisture content.

The organizational state changes within each EFC are not sufficient to functionally *explain* the flow of interest. Functional explanation requires interconnections among EFCs that represent the *control by an organizational state in one flow chain on an organizational state change in another flow chain*. In this situation there are six major interconnections (Fig. 27-1): (1) soil moisture control on the flow of numbers of potential settlers to settlers (WFC to IFC); (2) soil moisture control on the flow of numbers of settlers to successful families (WFC to IFC); (3) settler control on the flow of nonerodible to erodible soil (IFC to SFC); (4) successful family control on the flow of nonerodible soil to erodible soil (IFC to SFC); (5) runoff control on the flow of erodible soil to eroded soil (WFC to SFC); and (6) eroded soil control on the flow of rain to runoff via modification of the rock-to-soil ratio (SFC to WFC). This control then changes the amounts of rain becoming soil moisture and the amount of runoff becoming soil moisture, and the amount of soil that can hold moisture from either source.

We call these flow chains, together with their controlling interconnections, an **Ecological System** (ES) (Fig. 27-1). The ES is sufficient to both functionally describe and explain this particular set of relationships between isopod population dynamics and hydrologic and soil processes. In effect, we have combined the advantages of the "uniflow–unicurrency" and "multiflow–unicurrency" approaches into a "multiflow–multicurrency" ES. The ES retains the essential details about a flow of one measurable currency (e.g., the flow of numbers of isopods), with its major controls (e.g., soil moisture) while at the same time tractably linking different flows of very different, but measurable currencies (i.e., a flow of numbers with a flow of materials). Such an ES can then be used to understand the effects of organismal population dynamics on material fluxes and vice versa. However, in order to operationally connect population dynamics with material fluxes, we need to include information on the spatial and temporal scales at which the different types of flows represented by the EFCs operate and interconnect in the ES.

The Scales of the Flow Chains and the Ecological System

Isopod, water, and soil flow chains represent different types of flows operating across different spatial and temporal boundaries. Scalar properties can be added to the functionally descriptive properties of each flow chain by including the spatial and temporal extents at which each of the component organizational state changes within an EFC takes place. Scalar boundaries of each EFC are therefore determined by the collective boundaries of the component organizational state changes (Tab. 27-1).

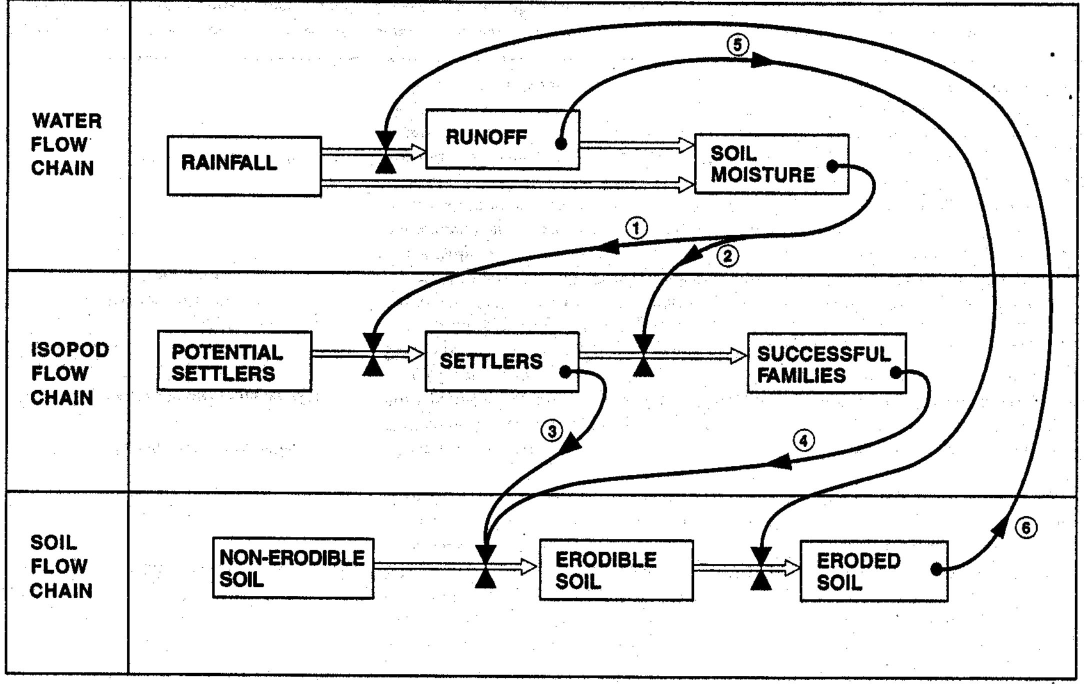

Figure 27-1. **The Ecological System** representing relationships among isopod population dynamics, soil erosion, and hydrology in the Negev Desert, Israel. Isopod population dynamics (a flow of numbers of organisms), soil erosion, and hydrology (material flows) are each represented as **Ecological Flow Chains** consisting of organizational state changes (open arrows, e.g., rainfall to runoff). The organizational state changes within a flow chain (three changes for water, two for isopods, two for soil) are collectively sufficient to describe the flow of a particular currency (amounts of water, numbers of isopods, amounts of soil). Explaining the flows requires controlling interconnections among flow chains. Here an organizational state within one flow chain controls an organizational state change in a different flow chain (shown as solid arrows with regulatory control points, ⧗). There are six such connections in this ecological system (see text).

Table 27-1. Spatial and temporal scale ranges of each organizational state change within the water, isopod, and soil flow chains in Fig. 27-1; and the rationales determining these scales

Ecological Flow Chain	Organizational State Change	Spatial Scale Range and Rationale	Temporal Scale Range and Rationale
Water flow chain	Rainfall to runoff	*Minimum:* Runoff generation from a patch of soil and its adjacent rock, about 5 m radius *Maximum:* Runoff generation over an entire watershed, **0.2 km – 0.2 km^2**	*Minimum:* Runoff event, a few minutes from a short, low intensity rain event *Maximum:* Runoff event, a few hours from a long, high-intensity rain event
	Runoff to soil moisture	*Minimum:* Soil moisture in a soil patch, a few **100 cm^2 to a few m^2** *Maximum:* Soil moisture in the soil portion of an entire watershed, up to 50% of the watershed area, 0.01–0.1 km^2	*Minimum:* Infiltration of runoff into soil, a few minutes to a few hours *Maximum:* Persistance of soil moisture from runoff, **about 2–3 years**
	Rainfall to soil moisture	*Minimum:* Soil moisture in a soil patch, a few **100 cm^2 to a few m^2** *Maximum:* Soil moisture in the soil portion of an entire watershed, up to 50% of the watershed area, 0.01–0.1 km^2	*Minimum:* Infiltration of rain into soil, a few minutes to a few hours *Maximum:* Persistance of soil moisture from rain, about a year
Isopod flow chain	Potential settlers to settlers	*Minimum:* Emigration distance, a few m radius *Maximum:* Emigration distance, **1 km radius**	*Minimum:* Emigrating and settling, **a few days** *Maximum:* Emigrating and settling, a month
	Settlers to successful families	*Minimum:* Family unit of the population in burrow, **0.75 cm radius** *Maximum:* Maximum emigration distance is the population boundary, **1 km radius**	*Minimum:* Raising a family, 6 months *Maximum:* Raising a family, **8 months**
Soil flow chain	Nonerodible soil to erodible soil	*Minimum:* Soil generated from burrow and surrounding feces by settlers and families, about **15 cm radius** *Maximum:* Soil generated in the soil portion of an entire watershed, up to 50% watershed area, 0.01–0.1 km^2	*Minimum:* Erodible soil formation from 1 day's digging by a family, or about 1 month's digging by settlers *Maximum:* Erodible soil formation from digging by a family during the **7-month** dry season when there is no runoff
	Erodible soil to eroded soil	*Minimum:* Erosion in a soil patch, a few 100 cm^2 to a few m^2 *Maximum:* Erosion in the entire watershed, **0.02 km^2 – 0.2 km^2**	*Minimum:* Runoff erosion of soil, a few minutes to a few hours during runoff events *Maximum:* Accumulation of erodible soil during the **7-month** dry season between runoff events

The collective scale boundaries of each flow chain are set by the minimum and maximum spatial and temporal values found across all component state changes, within that flow chain, and are shown in bold. Data on scale ranges come from studies referenced in the text.

Since the functioning of the entire ES is dependent on the connections among EFCs (as well as the EFCs themselves), the scales of these connections must also be identified. There are six connections among the three EFCs (Fig. 27-1), each of which has scalar properties that are determined by the spatial and temporal scales at which an organizational state on one EFC controls an organizational state change on another EFC (Tab. 27-2). The scalar properties of the entire ES are therefore the collective scale boundaries set by both the EFCs themselves *and* their interconnections.

Depicting Scalar Properties of the Ecological System

The spatial and temporal scales of the ES derived from the information in Tabs. 27-1 and 27-2 are shown in Figs. 27-2 and 27-3, respectively. Each organizational state change within an EFC, the boundaries of each EFC, and each connection between an organizational state on one flow chain that controls an organizational state change on a different flow chain, operates at distinctive and different scales. The ES is therefore multiscalar.

The maximum spatial scale of the WFC and SFC is the watershed (based on our question of interest we excluded the flow of water and soil out of a watershed via the wadi from consideration). However, the maximum spatial scale of the IFC encompasses a number of watersheds because of isopod emigration and immigration (Fig. 27-2). Because the WFC controls the IFC, water flow events that occur in one watershed can therefore affect isopod flows in another watershed(s) (via emigration). Because the IFC controls a critical portion of the SFC (erodible soil production) isopod flows in many watersheds can affect soil flows in a particular watershed (via immigration). Because the SFC feeds back onto the IFC via the WFC, and the IFC operates across a number of watersheds, both the soil and water flows in one watershed can indirectly influence soil and water flows in other watersheds, via isopod flows. Furthermore, the controls from one flow chain to another overlap more or less continuously across extensive spatial scale ranges. Thus large-scale events can influence small-scale events (e.g., runoff control on settlers to successful families) and small-scale events can influence large-scale events (e.g., settler control on nonerodible to erodible soil).

The maximum time scale of the IFC (which more or less corresponds to the annual life cycle) is slightly longer than that of the SFC. Both the IFC and SFC have a shorter maximum time scale than the WFC (Fig. 27-3). Consequently, the longest term fluctuations in isopod and soil flows will tend to operate over a shorter time frame than the longest term fluctuations in water flows. However, in comparison with the spatial ranges, the temporal scales of controls among flow chains are relatively discontinuous, with a more limited degree of temporal overlap (cf. Fig. 27-2). Consequently, longer term changes in water flow affect shorter term changes in isopod flows; water flow affects soil ero-

Table 27-2. Spatial and temporal scale ranges at which an organizational state within one flow chain controls an organizational state change in another flow chain, for the six controlling interconnections among flow chains (see Fig. 27-1 and text); and the rationales determining these scales

Controls Among Ecological Flow Chains	Spatial Scale Range and Rationale	Temporal Scale Range and Rationale
1. Soil moisture control on potential settlers to settlers	*Minimum:* Soil moisture at a settling site in a patch of soil, a few 100 cm^2 to a few m^2 *Maximum:* Soil moisture within the maximum emigration distance of potential settlers, 1 km radius	*Minimum:* Soil moisture accumulation sufficient to make a site for settling, 3 months of wet season in a wet year *Maximum:* Soil moisture accumulation sufficient to make a site for settling, 5 months of wet season in a dry year
2 Soil moisture control on settlers to successful families	*Minimum:* Soil moisture at a burrow site in a patch of soil, a few 100 cm^2 to a few m^2 *Maximum:* Soil moisture within the population boundary set by the maximum emigration distance of settlers, 1 km radius	*Minimum:* Soil moisture accumulation sufficient to raise a family, a wet season of 3–5 months in wet years *Maximum:* Soil moisture accumulation sufficient to raise a family, three wet seasons of 9–15 months in dry years
3. Settler control on nonerodible soil to erodible soil	*Minimum:* Settler production of erodible soil at settler burrow and adjacent feces from digging, 2 cm radius *Maximum:* Settler production of erodible soil at settler burrows within the maximum emigration distance of settlers, 1 km radius	*Minimum:* Settler production of a reasonable amount of erodible soil, about 15 days *Maximum:* Settler erodible soil production while they are settlers, about 1 month
4. Successful family control on nonerodible soil to erodible soil.	*Minimum:* Family production of erodible soil at family burrow and adjacent feces from digging, 15 cm radius *Maximum:* Family production of erodible soil at family burrows within the population boundary set by the maximum emigration distance, 1 km radius	*Minimum:* Family erodible soil production from 1 day's digging *Maximum:* Family erodible soil production during duration of family digging, about 7 months
5. Runoff control on erodible to eroded soil	*Minimum:* Runoff into a soil patch with erodible soil from a soil patch and its adjacent rocks, about 5 m radius *Maximum:* Runoff carrying eroded soil in the entire watershed, 0.02–0.2 km^2	*Minimum:* Runoff event, a few minutes to a few hours *Maximum:* Interval of about 7 months between runoff events in the dry season
6. Eroded soil control on rainfall to runoff	*Minimum:* Erosion conversion of rock to soil ratio at a soil patch and its adjacent rock, about 5 m radius *Maximum:* Erosion conversion of rock to soil ratio in entire watershed, 0.02–0.2 km^2	*Minimum:* Erosion conversion of rock-to-soil ratio, about 1 year, for high ratios, steep slopes, and shallow soil *Maximum:* Erosion conversion of rock-to-soil ratio, about 10 years, for low ratios, shallow slopes, and deep soil

Data on scale ranges come from studies referenced in the text.

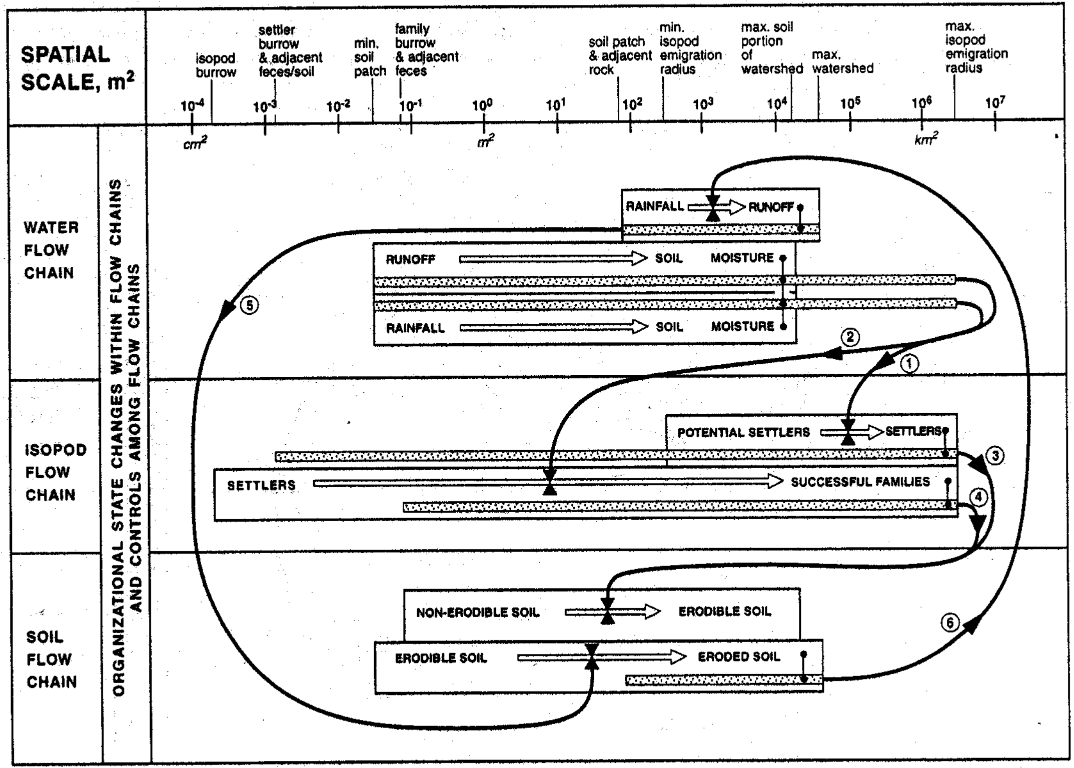

Figure 27-2. Spatial scales (m^2) of water, isopod, and soil flow chains and the ecological system consisting of these three flow chains and their six controlling interconnections (1–6; see Fig. 27-1 and text). Scale boundaries of organizational state changes within flow chains are shown as clear boxes containing open arrows that connect one organizational state to another (e.g., rainfall to runoff). Stippled bars represent the scale boundaries of the controls by an organizational state in one flow chain on an organizational state change in another flow chain. The symbol •–• connected to the stippled bar identifies the controlling organizational state. The solid lines and arrows, numbered 1–6, are the controlling connections, and the symbol ⧗ denotes the organizational state change in another flow chain that is being controlled.

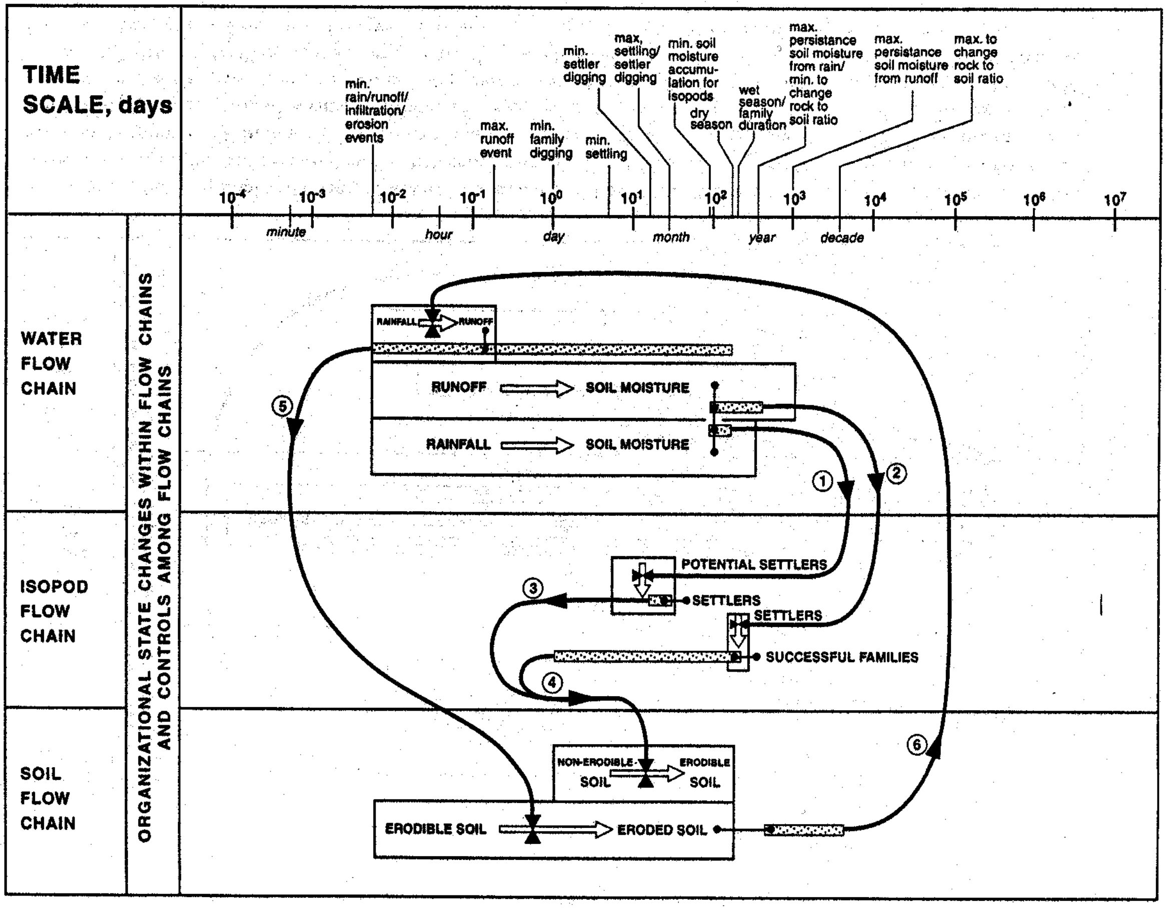

Figure 27-3. Temporal scales (days) of water, isopod, and soil flow chains and the ecological system consisting of these three flow chains and their six controlling interconnections (1–6; see Fig. 27-1 and text). For explanation of conventions and symbols see Fig. 27-2.

sion in the SFC over the same range of time scales; isopod flows affect erodible soil production in the SFC over the same range of time scales; and long-term changes in soil flow affect water flow over much shorter time scales.

It is clear from the multiscalar nature of the ES that a complete, functional understanding of these flows and their interactions cannot be achieved by studies at one, or even a few, spatial and temporal scales. However, the scalar properties of the ES can be explicitly defined and made operational in the field (see Tabs. 27-1 and 27-2).

UNDERSTANDING OTHER FLOWS OF NATURE

The multiflow, multicurrency, multiscalar ES connecting isopod, water, and soil flows (Figs. 27-1 to 27-3) illustrates the application and utility of the EFC and ES concepts for combining key attributes of the "uniflow–unicurrency" and "multiflow–unicurrency" approaches. The ES is functionally descriptive and explanatory. All of the components, flows, and scales of interaction are expressed in real, operational terms that can be directly measured in the field. Consequently, it is possible to develop qualitative and quantitative models of these relationships (see Shachak et al., 1994 for an example).

The isopod, water, and soil flow ES is just one set of interrelationships among flows of nature. However, this example indicates that the EFC and ES concepts should be broadly applicable to any set of functionally interconnected flows of nature. Furthermore, we speculate that the utility of the EFC and ES concepts can go beyond their value in representing a specific example of nature's complexity. The ES example we used has an underlying structure and properties that beg for comparison with other ESs. Such comparisons could provide generalizations about the structural and functional properties of ecological systems. Consequently, in the remainder of this chapter we provide general definitions, criteria, and guidelines for using the EFC and ES concepts to understand other flows of nature.

Definition and Criteria for Ecological Flow Chains

An Ecological Flow Chain is a series of organizational states connecting a measurable flow of materials, energy, structure, information, numbers, or any currency of interest. Changes in organizational states along a flow chain are collectively sufficient to functionally describe the flow of the currency, and are ascertained by measuring specified properties of defined biotic and/or abiotic entities that represent these organizational states. The boundaries of an EFC are determined by the collective spatial and temporal ranges over which the component organizational state changes take place.

The following criteria are used to construct an EFC, based on a question of interest: (1) the general type of flow (e.g., material, energy, structure, information, number of organisms or species). (2) The ecological criterion (sensu Allen and Hoekstra, 1992) that the flow represents (e.g., population = organism flow; community = species flow; ecosystem = material or energy flow; landscape = patch flow). (3) The specific measurable currency of the flow chain (e.g., numbers of a particular organism, number of species, amounts of a particular form of material [nitrogen (N), NH_3^+, soil, water, etc.], energy [solar, metabolizable, kinetic, etc.], information [genes, chemical signals, etc.], or structure [patch number, size, shape, etc.]). The specific measurable currency can be in an aggregated form (e.g., total N or species diversity or soil containing biotic and minerals) or not aggregated (e.g., a particular form of N, or developmental stage of an organism). (4) The type and number of organizational state changes that are necessary to functionally describe the flow (e.g., two in the IFC and SFC, three in the WFC). (5) The specified properties of the defined entities that must be measured to describe each organizational state change (e.g., the number of potential settlers to the number of settlers, the amount of erodible soil to the amount of eroded soil). The entities can be in aggregated form (e.g., soil is a biotic/abiotic aggregate; a successful family is an aggregate of individuals) or not aggregated (e.g., potential settlers). (6) The spatial and temporal boundaries of operation of each organizational state change and hence the collective boundaries of the entire flow chain (see Tab. 27-1).

In principle an EFC can be constructed for any flow. Although we have provided general examples of criteria 1–3, general examples of criteria 4–6 cannot be given without recourse to a specific question about a particular flow (see the three EFCs in our example).

Definition and Criteria for an Ecological System

An Ecological System is a set of at least two Ecological Flow Chains and their controlling interconnections that functionally describe and explain the flow of a measurable currency along at least one of the component EFCs—the focal flow(s) of interest that is selected based on the question being asked. Interconnections among EFCs are necessary to explain the flows. An interconnection represents the control by an organizational state on one flow chain on an organizational state change on a different flow chain. The ES has multiple flows, multiple currencies, and multiscalar properties that are determined by the collective scalar boundaries of each component EFC and the scales at which the controlling interconnections operate.

The following criteria are used to construct an ES, based on a question about the focal flow(s) of interest: (1) the number and types of EFCs necessary to explain the focal flow(s) (e.g., two other flow chains to explain isopod flows); (2) the number of interconnections among flow chains (e.g., six in our example); (3) the specific control points of the interconnections among flow chains (e.g., the organizational state of eroded soil controls the organizational state change from rainfall to runoff); and (4) the specific spatial and temporal scales at which interconnections operate (see Tab. 27-2). In principle an ES can be constructed for any set of interconnected flows of nature, but the ES structure and operation will always be determined by the question(s) asked. In our example, the ES structure was determined by asking how isopod population dynamics affected soil and water material flows and vice versa.

Deductive vs. Inductive Ecological Flow Chains and Ecological Systems

Our example shows that a substantial amount of information is needed to understand the interaction of flows. Most of the required information was at hand before we constructed the ES (i.e., an inductive example). However, the EFC and ES concepts can be used deductively. For example, we could have started by building an SFC- and WFC-based ES that had no IFC. By attempting to explain the SFC solely in terms of the WFC, it would become readily apparent that any agency markedly affecting the production of erodible soil would have to be included (in this case the IFC). Deductive construction of EFCs and their interconnections into an ES, using the criteria, can progressively reveal where information is missing and generates further questions that necessitate development of the ES.

Changes in Ecological System Structure

The structure of the ES entirely depends on the questions being addressed. Any change in focus requires changes in the ES. For example, if we were interested in the flow of soil out of the Negev, the WFC would have to include flash floods and water in wadis (temporary rivers) as organizational states. An interconnection between the WFC and SFC that represents the effects of flash floods moving soil down to the wadis, drainage basins, and the sea (with their spatial boundaries) would be needed. A temporal scale that included time periods with flash floods would be required, and so on.

CONCLUSIONS

Tansley's (1935) "basic units of nature" are complex, dynamic, interacting flows of organisms, materials, energy, information, and structure operating across multiple scales. Gaining tractable, operational, functional, and explanatory understanding of both component flows and entire units of nature is central to goals of enhancing subdisciplinary integration, advancing ecology and its application. Concepts that recognize and effectively deal with the multiflow, multicurrency, multiscalar properties of these units of nature can facilitate these goals. The Ecological Flow Chain and Ecological System concepts can be used to enhance concrete understanding of nature's complexity. The example we chose of interrelationships among isopod, water, and soil flows in the Negev illustrates the approach within the context of linking population and ecosystem ecology (i.e., organismal and material flows). However, we propose that these concepts can be used to understand interrelationships among many different flows linking many subdisciplines in ecology. We hope that our exemplification of the use of these concepts, together with their general definitions, criteria, and guidelines, will encourage ecologists to use these concepts to enhance ecological integration and understanding.

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