The Propagation of Ecological Influences through Heterogeneous Environmental Space

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Events or conditions occurring at one point in environmental space can have consequences elsewhere. For example, the management decision to feed elk over winter in the National Elk Refuge near Jackson, Wyoming, has led to an artificially large increase in the winter population of elk just north of the city (Figure 1; Boyce 1989). Natural elk deaths in winter have led to a concentrated supply of carrion that, in turn, has attracted a large population of ravens. But in the spring, the elk migrate northward to their summer ranges and the localized carrion disappears. The enlarged raven population also disperses northward, with individuals foraging expediently on whatever they can find, including songbird eggs and nestlings. As a consequence, nest predation is more severe in the Snake River riparian zone than it would be without winter feeding of the large, migratory elk population. Thus, an event or condition at the Elk Refuge (feeding elk) leads to propagation of nest predators across environmental space, with consequences (high nest predation) elsewhere (Dunk et al. 1994).

As another example, construction of a dam characteristically leads to sediment deposition in the impoundment. By reducing the sediment load of water coming through or over the dam, the capacity of downstream water to carry new sediment increases—the river becomes more erosive. As a result, the main stem of the river below the dam is excavated, thereby accelerating tributary downcutting throughout the entire drainage network (Figure 2). Tributary incision through the network accelerates slope movement, destabilizes vegetation cover, and degrades habitat. In this way, the new condition (the upstream dam) propagates geomorphological and ecological effects throughout the terrain below the dam.

These examples are two of a large variety of phenomena involving the transmission of cause and effect across environmental space. Such phenomena occur for many reasons and at many spatial and temporal scales. They clearly are ecologically important. How do ecologists address such phenomena?
ter was a primary attribute of such constructs. This interest was carried forward in the influential paper by Lindeman (1942) and expanded upon in E. P. Odum’s ground-breaking ecology text (1953).

Nonetheless, ecosystem literature devoted little attention to spatial interactions other than vertical fluxes of energy or matter between land and water surfaces and the atmosphere, or between water columns and sediments. Much less attention has been paid to lateral fluxes, with the exception of fluvial transfers out of watersheds (Bormann and Likens 1967). Even in those cases stressing outputs from watershed ecosystems, little attention is paid to where, exactly, exports go or to the impacts they might have at their locus of deposition.

Meanwhile, until the last 15 years, other areas of ecology have been even more centered on treating stands or communities as mostly isolated parcels in a matrix of neighboring parcels. For decades, the physical movements of resources, organisms, and disseminules between parcels, or between parcels and the outer environment beyond the immediate domain of the parcels, were minimized, treated abstractly, or ignored. The dominant view of ecologists was to focus on single, physical parcels and to discount—in fact, purposefully reduce—exchanges between them. This one-dimensional view of nature may have been a natural legacy of the integrated community viewpoint that has dominated American ecology since the beginning of the 20th century. Contrary to this site-centered tradition, however, applied areas of ecology—fisheries, wildlife, range and forest management—were forced by the realities of nature and management requirements to adopt flexible, spatial approaches.

This one-dimensional, site-centered focus of ecology began to change with developments in the late 1960s in island biogeography and, later, in landscape ecology, metapopulation ecology and genetics, and global ecology. For example, in 1987 Roughgarden and colleagues said,

> In both population and community ecology it is increasingly clear that data taken within a study site have limited power to explain what happens in the site. At some scale most ecological systems are open systems, and the control exerted by physical transport processes on population and community dynamics matches the effect of local processes, such as predation and competition among the residents of the site.

More recently, speaking on behalf of population demographics and genetics, Rhodes and Odum (1996) said,

> The belief that populations are in equilibrium and are density-dependent separate entities regulated by births and deaths is now considered dated. In many populations, immigration and emigration are more important as determinants than are births and deaths. There is general agreement that periodic local extinctions and recolonizations are common.

Similarly, Polis and colleagues (1997) spoke thus for community ecology:

> Ecologists are now aware that dynamics are rarely confined within a focal area and that factors outside a system may substantially affect (and even dominate) local patterns and dynamics. Local populations are linked closely with other populations through such spatially mediated interactions as source-sink and metapopulation dynamics, supply-side ecology, and source pool-dispersal effects. Our synthesis suggests several general principles: the movement of nutrients, detritus, prey and consumers among habitats is ubiquitous in diverse biomes and is often a central feature of population, consumer-resource, food web and community dynamics.

In the same vein, Aber and colleagues (1999) reflected on this point of view for ecosystems:

> The effects of landscape complexity, including the dynamics of the landscape pattern itself, have often been neglected in studies of ecosystem functioning. Most studies of atmospheric exchange processes with the land surface and of biogeochemical cycling in complex landscapes have assumed that the pattern of the landscape (e.g., vegetation mosaic) is constant. The question has been to determine how a given landscape pattern affects flows and pools of material and energy.

These statements suggest that many ecologists recognize the importance of interactions across heterogeneous space—that is, beyond the boundaries of sites, patches, or spatially delimited ecosystems. Today, at least some ecologists at every operational level of ecology recognize that lateral fluxes into and out of designated ecological units are at least as important as vertical fluxes between land or water and the atmosphere, or between sediments and water columns.

In spite of this general recognition and acceptance, it appears that few ecologists have explicitly considered the prevalence and variety of these interactions, and even fewer know...
how to formally treat these phenomena. With certain exceptions, methods for dealing with fluxes and movements either theoretically or empirically have not yet been fully realized, even in landscape ecology (Wiens 1992, 1995, 1999). Exemplary exceptions are the work of Costanza and colleagues (1990) and of researchers who are developing spatially explicit individual and population models (Dunning et al. 1995). Meanwhile, conceptual frameworks (Egenhofer and Golledge 1998) and empirical methods (NCGIA 1996) are practiced widely in other environmental sciences such as geography, hydrology, and epidemiology.

In order to provide a systematic treatment of the propagation of ecological influences through environmental domains, we propose appropriate language for discussing them, briefly describe a general heuristic model, and suggest methods for studying them with realistic, explicit, spatial representations. The general question we seek to answer is, How do events or conditions occurring at a particular position in environmental space lead to consequences elsewhere in environmental space?

A conceptual framework and lexicon for spatial interactions

An inclusive discussion of the transmission of cause from one place to an effect somewhere else must include the full range of global environments and extents, or scales. Such inclusivity requires careful consideration of language. Some words normally used for this subject are problematic, forcing adoption of more neutral language.

For example, inclusion of aquatic and marine systems in our treatment renders landscape inappropriate. This subject does not apply only to terrestrial environments. In fact, landscape is problematic for other reasons as well. It is laden with special meanings related to scale and conceptual organization that interfere with a flexible and open approach to this topic (Wiens 1999). Landscape ecology is an exciting and vital subdiscipline of ecology that makes important scientific and practical contributions to theoretical and applied ecology. Nevertheless, we avoid the word landscape in favor of the more neutral and inclusive term environmental space (or volume) for the arena in which the phenomena we address occur.

Another problematic word is interactions, one of the central elements of some definitions of ecology. Dictionary definitions clearly and consistently state that the term interaction explicitly requires reciprocity between elements. In fact, few phenomena of ecological interest actually involve reciprocity. To avoid etymological and common usage criteria of reciprocity, we substitute influence, a more general term that encompasses one-way cause and effect phenomena, although that word too is laden with semantic problems, such as the sense of intangibility.

How do causes at one locus get transmitted to produce effects somewhere else? Somehow, something is moved across space. We use the term propagation as a general term for...
such phenomena. Transmission or conveyance are appropriate synonyms. Collectively, the propagation of ecologically relevant causes from points of origin to loci of effects can be viewed as having four elements: (1) a temporary, initiating cause, or a chronic condition somewhere in the environmental space; (2) some entity transmitted from origin to destination; (3) a transmitting vector that carries that entity from origin to destination; and (4) a consequence of the propagation (Figure 3). Each of these four elements has its own taxonomy. These taxonomies contribute to an immense diversity of propagation phenomena. Part of the problem in organizing this topic is structuring all of these dimensions. A brief review of each of these elements follows.

Figure 3. A conceptualization of the critical components of ecological influences through environmental space involved in propagation, as defined and reviewed in the text.

Initiating events or chronic conditions. Conceivably, any temporary event or long-term condition in the spatial domain could influence something elsewhere. The range of possibilities is virtually endless. For that reason, the analysis of initiating causes can proceed only as far as defining categories. We think that the following seven categories provide a taxonomy of initiating causes adequate for our present purpose.

1. The kind of environment, in the broadest terms, in which the event or condition occurs. There are substantial differences in the kinds of propagation phenomena dominating terrestrial, aquatic, and marine environments. Subdividing on these grounds vastly limits the number of propagation vectors likely to occur in a specific case. Of course, environments can be subdivided within each of these broad possibilities.

2. Temporary, discrete event or chronic condition. Lightning strikes, fungal infections, windstorms, and landslides are all short-term, discrete events, whereas geological outcrops or spring upwellings are long-term conditions. Both can influence parts of the surrounding environmental space. Discrete events and chronic conditions are regarded quite differently in their spatial–temporal dynamics.

3. The spatial extent of the initiating event or condition. The extent of discrete initiating causes varies in both space and time. Both dimensions have to be specified to properly characterize the cause, and there is no necessary proportionality between the extent of the cause and the extent of the resulting effect. A howler monkey’s call, at its origin, is very localized in space to a volume of a few cubic centimeters, whereas its reception may extend over several square kilometers. In contrast, the spatial extent of a serpentine outcrop can range from square meters to square kilometers, but its area of geochemical influence may only be slightly larger than its originating extent.

4. Duration of discrete events. Discrete events have characteristic durations ranging from milliseconds, as with lightning strikes, to growing seasons in the case of insect outbreaks. How, then, does one decide whether an event is discrete or chronic? That distinction has to be made in terms of the consequence of the event. If the duration is shorter than the characteristic time constant of the impacted element of the system, such as a dominant plant life span, it would be discrete, rather than a chronic event. Here, as elsewhere in ecology, effects as well as the causes shape definitions.

5. Periodic or aperiodic character of the discrete event. Discrete events may be periodic, tending to recur at regular intervals. If so, their periodicity may vary widely from seconds to minutes, as with firefly flashes, to tens to hundreds of thousands of years, as with Milankovitch cycles. Other events, such as rock falls, may be more chaotic in their temporal recurrence. Admittedly, the discrimination of periodic behavior is sometimes difficult to detect, such as with the Pacific Decadal Oscillation.

6. Abiotic or biotic origin. Some initiating events or conditions, such as blow-downs or springs, are all, or primarily, of abiotic origin. Others may be primarily biotic with abiotic manifestations, such as eutrophication impacts accompanying waterfowl congregations in lakes and wetlands.

7. Natural or anthropogenic origin. Human effects cannot be ignored in this discussion. It is possible that some anthropogenic impacts, like management fires, may simulate natural events, but many, perhaps most, anthropogenic effects are fundamentally different from those initiated by natural phenomena. Road construction on steep slopes has little if any similarity to natural geomorphological events in mountainous terrain, and there are few, if any, analogues to toxic waste dumping in nature.

Entities propagated. In order for a cause to produce an effect somewhere else, an entity must be transmitted across space. What are these entities and what are their relevant properties? A starting point is to classify entities as some form of energy like the kinetic energy of wind, matter like the flow of soil nutrients through the vadose zone, or information like the flux of spores. It quickly becomes evident, however, that entities are almost always combinations of energy, matter, and information. Again, their categorization becomes defined by their consequences (Figure 4).

It is difficult to imagine any entity that might not have some information content. Abiotically generated light and sound are given as examples of entities in the energy cell of Figure 4, and of nonreactive inorganic materials in the matter cell. But each of these might be interpreted as having information content as well. Sunlight contains spectral and timing information for organisms capable of sensing it, and phytoplank-
ton can determine the difference between nitrate and ammonium ions in their surrounding medium. Thus, the pure energy or matter cells might actually be considered empty cells.

Conversely, there can be no entity consisting of pure information. Information, whether signals or genetic, must be encoded in either energetic terms, such as sound waves, or in material terms, such as pheromones or genetically dispersable materials like spores. Thus, the pure information cell is an empty cell (Figure 4). It will always be combined with energy, matter, or both.

Figure 4. Propagated entities can be defined as energy, matter, or information, depending on outcomes. The essence of an entity must be defined in terms of its impact within the context of the phenomenon under analysis. Entities of pure energy or material are possible, but almost invariably they are combinations of another and information, residing in the overlapping ovals of this figure. Information, on the other hand, must always be conveyed in combination with energy or matter. Thus, pure information is an empty cell.

In one fundamental way, all entities must be associated with energy. For an entity to be propagated, it must be in motion. Matter in motion has momentum, so that all material entities possess at least the energy of momentum. Matter can possess energy in other ways as well. Parcels of water and air bear sensible or latent heat that can import or consume energy at their points of influence. Thus, a parcel of air can be relevant as an entity from a material point of view (its molecular composition), from an energetic point of view (its momentum or sensible and latent energy), or possibly from an informational point of view (as an indicator to an organism of the direction toward warmer or cooler conditions).

How best to characterize an entity depends on the operational nature of the entity when it reaches the target in the environmental space. As with many things ecological, definitions are situational. The key is to start at the endpoint—the consequence—and do the defining there. Given these philosophical caveats, we will describe some entities in order to illustrate their range of possibilities.

Some entities defined in energetic terms are kinetic energy (momentum of moving mass), sensible heat (thermal energy of mass measured as temperature), latent energy (energy of evaporated water in air), and chemical energy (bound energy of reduced substances, such as organic matter). Transport of air by wind might be measured in all four of these terms, but usually its influence is specified with respect to the impact of interest, whether it is knocking down trees, cooling leaves, evaporating water from vernal pools, or conveying reduced carbon compounds such as hydrocarbons. High velocity, mass-wasting phenomena such as landslides and snow avalanches might be measured in terms of kinetic energy as well as relocated material, whereas a slow velocity mass-wasting phenomenon such as soil creep might be measured in terms of its material transfer rather than its kinetic energy. Other energy-bearing entities are electromagnetic radiation, sound, and bioelectrical fields. These may have abiotic significance of their own (e.g., driving photosynthesis) or may be very important in terms of signaling between individuals and perception/deception activities of animals.

The second general category of entities is matter, the case in which the mass of the entity transported, whether it is gases, liquids, solids, or dissolved and suspended solids in water, is the property of consequence. Most examples of propagation involve matter. Even sound involves compression waves passing through media. Water running over slopes, down channels, and through soils and aquifers includes the mass of all three—liquid, solids, and gases. Colluvial movement of hill-slope materials or snow involve mostly solid matter but may include substantial amounts of water. Wind involves transport of air parcels and currents entail water parcels. In the case of a flame front, the entity is both the thermal energy of the flame plus the mass of the hot gases. Whether it is the mass or the energy that is the primary affecting entity depends on the impact of interest. Wind can transport toxic gases or it can blow down trees. In the first case it is the mass and associated physiological effect of the toxic gases that is important; in the second case it is the kinetic energy.

The third general category of entity, and perhaps most interesting for biologists, is information. Information may be divided into signals or genetic information. We apply the term signals to instances of propagated stimuli not involving transfer of genetic material. Secretions of pheromones are instances of signaling using matter. Light emissions by fireflies are signal information conveyed by electromagnetic radiation through the atmosphere. Electromagnetic radiation is, in this case, both the vector and the entity. The mating calls of whales are signal information conveyed by sound energy through the aqueous medium. Light, as in the firefly case, and sound, as in the whale calling case, are both the vectors and the entities.

In contrast, genetic information carried by spores, pollen, seeds, other vegetative propagating material, and eggs and dispersing animals is biochemically encoded as matter (DNA) along with a small (in the case of pollen) or large (in the case of dispersing breeding animals) amounts of associated free energy. Mass, energy, and information are incorporated in these items, but if it is the propagation of the genetic information that is the consequence of interest, then the entity is defined as information. We acknowledge that an ambiguity exists
Vectors propagating entities. Some transmitting agent must convey or propagate an entity from its place of origin to its place of action. We term these agents vectors. Definition of vectors depends on where one wants to focus across the gradient of ultimate to proximal causality. We present a list of 11 vectors in Table 1 that are useful for this level of discussion. These lie intermediately between ultimate causes (such as solar nuclear reactions) to proximal causes (such as a particular rock fall). Four of these vectors are illustrated in Figure 5. Nontidal currents control fluxes of heat, salinity, nutrients, and organic carbon throughout the oceans. Rockfalls are just one of many examples of gravity-driven, colluvial transport in areas having relief. Large migratory mammals are a particularly dramatic example of animal locomotion, and sand dunes are a substantial manifestation of the power of wind transport.

Most of the vectors in the right column of Table 1 can be subdivided into increasingly detailed subcategories of the general phenomenon. For example, fluvial transport can be subdivided into hydrometeors and nonhydrometeors, between surface and ground water, between saturated flow and unsaturated flow, and so forth. Also, Coriolis force is an important ingredient of many fluid flows (e.g., wind, tidal currents) but is treated as an element of gravity here. Both electromagnetic radiation (light and radiant heat) and sound stand apart from other transport vectors in that the vector is also the entity propagated.

All of the vectors have their own properties and arenas of greater or lesser importance. Obviously, tidal currents are irrelevant on land and relatively unimportant in the centers of oceans, but they are extremely important in coastal zones. Molecular diffusion occurs in all environments and over enormous distances, but is only important as a vector over short distances—millimeters to centimeters. The role of wind varies geographically but it is important in marine, aquatic, and terrestrial environments within the thin interface where the atmosphere meets water or land surfaces.

Consequences of propagation. Propagation of entities by vectors will have consequences, however important or trivial. Sheet wash across a field removes soil from the wash zone and deposits it at the base of that zone or in a stream channel. Deposited spores infect susceptible plants downwind of their source. Fire combusts fuel across its field of travel so that the consequence is broadly distributed. A territorial call by a mating bird will have a consequence only for other males of the same species within hearing. There are as many possible consequences as there are permutations of causes, entities, and vectors across environmental domains.

A consequence may become another initiating cause that will engender propagation of another entity to another location. Thus, a secondary, or even concatenating, series of causes and effects may result. In such a case, the consequence becomes the cause so that the cycle of propagation illustrated in Figure 3 may be repeated.

A general model for propagation of influences in space and time
In his aptly titled paper, “Process dynamics, temporal extent, and causal propagation as the basis for linking space and time,” Kelmelis (1998) provides a general analysis of the relationship between space and time for process modeling in spatial–temporal contexts. As he points out, space and time are inextricably linked in the propagation of cause to consequence, and spatial extents resulting from propagation events are positively related to the time since their initiation (Figure 6a). But the range of extents also depend on the magnitude of the event, the temporal extent of the causal event, and environmental factors influencing the propagation rate. For example, the extent of spread of a pathogen will generally increase over time but the exact rate and trajectory of spread, and thus extent and spatial distribution, will depend on

Table 1. Ultimate and medial vectors responsible for propagation of ecological influences at two levels of causation.

<table>
<thead>
<tr>
<th>Ultimate causation</th>
<th>Medial causation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solar radiation, radiogenic heating</td>
<td>Molecular diffusion</td>
</tr>
<tr>
<td>Solar radiation, gravity</td>
<td>Fluvial transport</td>
</tr>
<tr>
<td>Radiogenic heating, gravity</td>
<td>Colluvial transport</td>
</tr>
<tr>
<td>Solar radiation, gravity</td>
<td>Glacial transport</td>
</tr>
<tr>
<td>Solar radiation, gravity</td>
<td>Sedimentation</td>
</tr>
<tr>
<td>Gravity</td>
<td>Tidal currents</td>
</tr>
<tr>
<td>Gravity, solar radiation</td>
<td>Nontidal currents</td>
</tr>
<tr>
<td>Solar radiation, gravity</td>
<td>Wind</td>
</tr>
<tr>
<td>Miscellaneous events, solar radiation (via</td>
<td>Sound</td>
</tr>
<tr>
<td>animals)</td>
<td>Electromagnetic radiation</td>
</tr>
<tr>
<td>Solar radiation (directly and via animals)</td>
<td>Animal locomotion</td>
</tr>
<tr>
<td>Solar radiation</td>
<td></td>
</tr>
</tbody>
</table>

Note: Determination of ultimate and medial causation status is limited to Earth’s domain based on energetic sources and specific carriers.
weather and dispersal conditions. Similarly, a snow avalanche will cover more ground with time, but its full “run-out” distance will depend on slope steepness and vegetative resistance to flow. These environmental factors are defined by Kelmelis as “resistance” or “viscosity” to causal propagation through a particular medium and to attenuation processes.

It is not necessary to review the entire derivation of Kelmelis’s general exposition of the propagation of events to appreciate a general expression of it, as provided below:

\[ E_\text{t} = f(M, E_t, t_e, V_{cp}, A), \]

- \( E_\text{t} \) = spatial extent at time \( t \),
- \( M \) = magnitude of event,
- \( E_t \) = temporal extent of the event, \( t_e \) = elapsed time from event initiation, and
- \( V_{cp} \) = velocity modified by
- \( A \) = attenuation factors.

This conceptualization is diagrammed in Figure 6a, in which the propagation of an event at a point in time extends outward in space through slices of time represented by the \( y \)-axis until it reaches time \( t \), shown as the circle of propagation. The propagation mechanics are like those for unfocused sound or diffusion. The environmental \( x-y \) space is treated as homogeneous in Figure 6a but is divided into two types in Figure 6b, one having a lower velocity coefficient. In that case, propagation is slower in the environmental space on the right so that the propagation field at time \( t \) takes on an irregular shape.

This conceptualization by Kelmelis serves as a general model for all propagation phenomena. The spatial extent of the initiating event (e.g., different-sized hillside springs or insect outbreaks), magnitude of the event (e.g., intensity of a lion’s roar), temporal extent of the event (duration of a mating display), elapsed time from event initiation (i.e., position on the vertical axis), velocity (dependent on vector and medium), and environmental attenuation factors (e.g., slope angle for gravity-driven movements) will control the exact distribution of a propagation at any point in time. Variable velocity coefficients are of particular interest because they represent the effect of variable environmental space on propagation direction or area of influence. For example, snow avalanches will be directed along the steepest slopes and paths of least resistance, while light emanating from brightly colored feathers of a bird of paradise will best be seen in forest openings where foliage least interferes with light transmission.
How can propagation phenomena be modeled for particular cases? The general model outlined above may serve most heuristic purposes, but this topic also has special importance for the application of ecological principles to particular cases. Spatially dynamic models facilitate prediction and allow testing of the sensitivity of phenomena to changes in specific driving variables. How can we organize the rules for particular propagations so that phenomena can be simulated by models?

While it is possible to predict system behavior at points and along one-dimensional gradients with relatively simple formulations, it is more difficult to do it in two or three dimensions. Dynamic modeling with some form of spatial distribution system like GIS (geographic information system) is the most effective means for predicting and learning about propagation phenomena. This is a common approach in landscape ecology and, more broadly, in geography, geomorphology, hydrology, epidemiology, and fire ecology. Essentially, these approaches combine transport models with realistic representations of the environment in a GIS (Maguire et al. 1991, Goodchild et al. 1996, NCGIA 1996).

Organizing the problem, the data, and the system for modeling propagations consists of the following steps:

Step 1: Define the phenomenon in terms of the four components (causal event, entity, vector, and consequence).

Step 2: Define the requisite environmental space, which must encompass the area that incorporates all the essential factors in the process and the extent of the propagation. This becomes the model domain.

Step 3: Determine how the environmental domain should be represented for appropriate modeling.

Step 4: Acquire appropriate spatial data necessary to provide information for controlling the transport process.

Step 5: Select and modify an appropriate transport model for the phenomenon of interest.

Step 6: Integrate the transport model and the GIS to provide spatially distributed input and output.

Step 3, technically the “data model,” is extremely important. How we represent the environment has enormous ontological significance, as it determines the way phenomena are defined and given significance (Raper 1999). Landscape ecologists and other geographically mediated scientists typically use one of four representations of two-dimensional space: (1) tesselation, (2) patch-matrix, (3) patch mosaic, or (4) patch-corridor–ecotone representation (Figure 7). Regardless of what representation is used, the domain must be sufficiently large to encompass the full functionality of the phenomenon in question, and the grain of the subunits must be sufficiently small to represent all the environmental features critical to invoking important processes. In fact, most propagation phenomena occur in three-dimensional space, hence the title of this article: “The Propagation of Ecological Influences through Heterogeneous Environmental Space.”

For aquatic or marine systems, it is essential to portray and model those environmental volumes with three-dimensional software and visualization tools—tools that are not generally available. When propagation over time is taken into account, modeling is really a four-dimensional problem (Aber et al. 1999). For the most part, however, ecology is still at the stage where processes are compressed into a two-dimensional representation of environmental volume. Therefore, in the rest of this article we will assume two-dimensional environmen-
Environmental data can be organized in several ways. Sometimes they are organized as meshes, lattices, or arrays of triangles, net elements, hexagons, or polygons, which can be regular or irregular. Collectively these are termed tesselations (Maguire and Dangermond 1991, Burrough and McDonnell 1998). Regular, rectangular grid arrays are referred to as “raster” data; these grid arrays are so common that “raster” is often used instead of “tesselation” in discussions of contrast with “vector” data structuring.

Alternatively, when information exists about the location of specific objects or aggregated elements relevant to the phenomenon of interest, such as field boundaries or stream networks, they are usually represented in GIS as a record of coordinates for line segments and points. This efficient data structure is known among geographic information scientists as vector data.

Tesselation is probably the most neutral mode of data organization, in that it assumes no higher level ecological organization but accepts continuous or discontinuous data representations for any of the environmental themes involved in the phenomenon in question. This is a good approach for representing sheet wash or wind fields, for example, although some spatial accuracy may be lost when curvilinear features are forced into rectilinear arrays of large grain size (Figure 7a). On the other hand, there is much to be gained for some problems by specifically recognizing aggregate features that are relevant to the process. For example, it would be foolish to ignore the pattern of fields in an agricultural landscape when a phenomenon such as animal foraging is driven by spatial organization dictated by those fields.

Choosing the appropriate transport model (step 5) can be difficult. The tradition for transport modeling in ecology is limited (Aber et al. 1999), so in most cases ecologists have to turn to other sciences. The literature is somewhat confusing, with partially overlapping modeling approaches such as finite element, finite difference, cellular automata, stochastic, process-based, event-based, individual-based, agent-based, and object-oriented modes. A directory of spatially dynamic transport models, with model metadata containing commentaries on their requirements and limitations, would be a useful tool for ecologists. Meanwhile, the definitions and descriptions of model types described by Mitasova and Mitas (1998) and Wegener (2000) are helpful.

Integrating particular models and GIS (step 6) also requires specialized skills not necessarily a part of an ecologist’s toolbox. For most ecologists, dynamic spatial modeling requires collaboration with others to achieve their goals in the same way that ecologists team up with statisticians, geneticists, soil scientists, and programmers to solve problems requiring knowledge and skills that go beyond those of most ecologists.

Some examples. This text has so far addressed the propagation of ecological influences in conceptual terms. The following applications are examples that may aid in understanding and appreciation of these concepts.

Sound transport. To illustrate the approach outlined above, we offer two examples. The first is a model developed by Kirsten Parris to demonstrate the transmission of sound. Sound and hearing are important parts of the environment in which most animals live. Sound is propagated by compression waves through air, water, soil, and rock. Some sound, like that produced by wind in trees, may be just background noise to most animals. Other sounds, such as species-specific territorial calls, are highly refined propagation processes laden with information. The physics of sound is well known, but modeling it for natural environments can be complicated. Sound transmission is affected by materials surrounding the primary medium of transport. For example, soil, snow, or water affect sound transmitted through the air above them. Sound is also altered by changes in medium density, such as stratification resulting from temperature inversions, and it is attenuated by interference of intervening objects in the primary medium, such as vegetation or topographic features (Bradbury and Vehrencamp 1998).

The sound model simulates mating calls of the male northern spring peeper Pseudacris crucifer crucifer and is based on research by Wilczynski and colleagues (1984), Gerhardt (1975), and Brenowitz and colleagues (1984). For this system, no topographic data were needed because the domain was confined to a flat marsh. Spatial data for the distribution of trees, shrubs, and ponds in the graminoid matrix of the marsh were needed, however, because these objects influence the propagation of sound. Therefore, the GIS data representing the two-dimensional spatial environment is a patch-
mosaic data model in raster format, with ponds and woody plants as patches in the graminoid matrix. The user of this model can dictate the location of the calling male spring peeper and whether he is situated on the ground level or up on the graminoid vegetation. Sound travels much farther when initiated away from the ground. The hearing of female peepers is more sensitive to male frog calls than to the calling male. Sound propagation is greater for females than for males. The male and female detection thresholds as well as the call intensity can be adjusted by the user.

The intensity of the sound at particular distances depends on its attenuation by the ground surface and larger vegetation. However, when sound travels over water, signal amplitude can increase by 6 dB above that expected from spherical spreading, thereby doubling the distance of propagation (Allmon 1991, Allan and Flecker 1993, Forrest 1994). Thus, the effective perception distance of a female depends on her spatial relationship with ponds as well as with the calling male. The sound propagation calculations are done with a computer program written in the C programming language coupled with a GIS software named ArcView (a product of ESRI, Redlands, California) GIS. An example of output is shown in Figure 8.

**Transport by wind.** Our second example is a wind transport model. Wind is an important transport vector for many things: momentum, gases, sensible and latent energy, detritus, dispersing animals, spores and pollen grains, sand, or snow. Transport of snow by wind may seem esoteric to many ecologists, but in fact is important in windy environments receiving copious snow and where there is no tree cover to diminish the wind. Redistribution of snow by wind in these cases exerts fundamental controls on the spatial distribution of structural and functional attributes of communities and ecosystems. Such is the situation in the treeline and alpine environments of the Rocky Mountains.

Another model is designed to predict the redistribution of snow for a treeline area in the Medicine Bow Mountains, Wyoming. The modeling domain is a broadly arching ridge called Libby Flats, located at 3,100–3,300 meters elevation, extending north–south, perpendicular to the prevailing wind. Here, 70% to 80% of the annual 89–125 centimeters precipitation falls as snow and the mean wind speed in winter is 10 meters per second. From November to May, wind redistributes snow from open areas into large drifts up to 7 m deep. The vegetation of Libby Flats consists of scattered trees and shrubs embedded in a matrix of subalpine meadow vegetation. The trees and shrubs are spruce and fir (Picea engelmannii Parry and Abies lasiocarpa [Hook] Nutt.), which occur as low krummholz patches or as erect ribbon forests. Both forms cause accumulation of snow on their lee sides, thereby playing a large role in wind's redistribution of snow across this terrain.

This model was adapted by Hiemstra (1999) from a snow transport model created by Liston and Sturm (1998), SnowTran-3D. The original domain was 2.5 x 2.5 kilometers on Libby Flats, but for demonstration purposes we reduced the domain to a central area of 1 x 1 km. Spatial data included raster layers for topography and heights of woody vegetation. Meteorological data on snowfall, wind velocity and direction, and temperature were collected at nearby stations and modified for the orientation of the modeling domain. The original model was driven with actual meteorological data, but to demonstrate process controls we have modified the model of Hiemstra (1999) so that the user can vary duration of run, snowfall amount, wind direction, and velocity.

Several kinds of output are available, but Figure 9 shows the net result of wind erosion and deposition of snow for conditions of wind from the NW at 15 m/s and snowfall of 10 cm
per day over a 10-day model run. Topography controls the distribution of spatially large drifts, but tree vegetation imposes another level of depositional complexity, and the largest drifts are found directly leeward of rows of trees on the terrain. Areas with very heavy accumulated snow have short growing seasons and scanty vegetation. Areas from which snow has been eroded have scanty vegetation because of lack of moisture. Between these two extremes lies a continuum of snow-free growing season time and soil moisture supply. Together, these factors control the distribution of species, productivity, and soil properties of this landscape.

**Propagation of ecological influences: Linkages through space**

Much early terrestrial ecology concentrated on the internal dynamics of freestanding communities or ecosystems. Vertical exchanges were recognized and estimated but horizontal exchanges or transmissions were given little attention. This was not true for aquatic and marine ecology, in which the lateral advection of materials was fundamental to understanding the structure and function of defined units in the water. With the onset of island biogeography, metapopulation ecology, and landscape ecology, lateral transfers began to get explicit attention.

If one considers propagation phenomena occurring in all biomes and at all spatial and temporal scales, it becomes evident that environmental space is traversed by enormous numbers of propagation events, each with its own properties of causal events, vectors, entities, and consequences. Nonetheless, ecologists have rarely, if ever, tried to organize these phenomena in a systematic way for formal analysis and comprehensive instruction.

The system described in this article is one such attempt, however. The diagram in Figure 10 is a semiabstract expression of all of the propagations that can be going on across a section of environmental space in a short window of time. These propagation phenomena have influences that may be transitory, or they may have long-term impacts. This abstract landscape may bear marks and patterns (not shown) resulting from propagations that occurred in the past. These long-lived consequences may range from something as subtle as an unusual allele in a local population introduced by a pollen grain of far distant origin, to something as obvious as rows of avalanche and debris flow stripes on steep mountain flanks. Collectively, propagations of the past and present represent the means by which ecological influences bind ecological elements together across environmental space, often as ghosts of propagations past.

Borrowing from string theory (Greene 1999), we find it useful to imagine, by analogy, that propagation phenomena are like invisible strings extending throughout the biosphere that transmit, or have transmitted, influences with different
intensities, frequencies, and periodicities. To paraphrase, these are the ties that bind environmental domains in ecological ways. Analogies are dangerous and we would not wish to push this imagery very far. Nevertheless, incorporation of propagation phenomena may contribute to a higher order theory about ecological influences that helps us understand how nature is organized and altered over time.

Acknowledgments
We thank the Andrew W. Mellon Foundation for support of the work underlying this article and the National Center for Ecological Analysis and Synthesis for support in preparation of the paper. We also thank John Wiens for a helpful review and Kirsten Parris and Philip Polzer for development of the two interactive models.

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