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Reciprocal Cause and Effect Between Environmental Heterogeneity and Transport Processes

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Abstract

The objective of this paper is to explore the relationships between environmental heterogeneities and the flows and movements that suffuse through all environments. Flows and movements are treated as propagations of ecological influence through environmental space. Propagations are composed of four elements: (1) initiating events or conditions, (2) transport vectors, (3) transported entities, and (4) deposition or impact processes. All four elements have multiple dimensions in type and scale, but vectors are the most convenient means of discussing these phenomena. At a medial level of causation, 10 major vectors are convenient descriptors. These vectors are molecular diffusion; transport by fluvial, colluvial, or glacial modes, gravitational sedimentation, currents (tidal and extratidal), wind (with fire as a special case) agencies; and by electromagnetic radiation, sound, and animal locomotion. Obviously, each of these vector types has different behavior. Propagations can be initiated, or modified by, environmental heterogeneities. But also, propagations can create, maintain, and destroy heterogeneities. Thus, reciprocal cause and effect relationships exist between propagations and environmental heterogeneities. Analysis and understanding of these reciprocal interactions between propagations and heterogeneities requires some understanding of the mechanics of propagations, whether they involve wind, waves, or wallabies. In the same sense, analysis and understanding of how environmental heterogeneities alter propagations requires an appreciation for the global range of heterogeneity types, whether they are ripples, runnels, or run-on patches. Spatially explicit two- and three-dimensional models of propagations in heterogeneous environments are useful ways to develop understanding and, with caveats, to predict how processes and patterns interact. Some of the representational issues of building such models are reviewed in this paper, and three model examples are described.

Introduction

Although ecology has always been a geographically based science, for many decades basic ecological research tended to have a point-model focus. With some important exceptions (e.g., Watt 1947), this was reflected in the emphasis on putatively homogeneous sites, whether stands or watersheds, as the appropriate representation of nature (Wiens 2000; Reiners and Driese 2004). This was not true in applied areas of ecology such as forestry, wildlife, fisheries, and range sciences where spatially distributed representations of nature were imperative. Point models were of little use for predicting habitat usage by deer or the dispersal of white pine blister rust. This perspective has changed for basic ecology in the past two decades, however, as the point-model view of nature has largely given way to a spatially heterogeneous representation of nature (Turner et al. 2001; Chapin et al. 2002; Reiners and Driese 2004). With the advent of new foci such as landscape ecology, conservation biology, and earth system science, and with the practical application of tools for acquiring and managing spatial data, the conceptualization of nature and the practice of basic ecology have made the heterogeneous domain the primary focus (Turner et al. 2001).

A benefit of adopting a spatially distributed view of nature is an easier incorporation of flows and movements into our visualization and treatment of a spatially heterogeneous environment. Transport processes—so intrinsic to the way nature operates—underlie many of the more interesting and important aspects of ecology. Personal experiences tell us that transport processes are influenced by environmental heterogeneity. By stepping around the corner of a building on a windy day, for example, we notice significant changes in our bodily comfort. A spatial approach to ecology now allows us to appreciate, analyze, and model how spatial heterogeneity and transport phenomena are reciprocally related.

The objective of this paper is to review how flows and movements of different kinds affect, and are affected by, environmental heterogeneity. This paper is organized into six sections: (1) how transport phenomena act as propagations of ecological influence, (2) how transport processes are affected by environmental heterogeneity, (3) how propagations may produce, maintain, and destroy environmental heterogeneity, (4) issues in the spatial representation and modeling of propagations, (5) three examples of propagation modeling in heterogeneous environments, and (6) how a propagation perspective might influence our conceptualization of nature and ecology.

Transport Phenomena as Propagations of Ecological Influence

Flows and movements can be generalized as propagation phenomena entailing four components: (1) initiating events or chronic conditions, (2) a

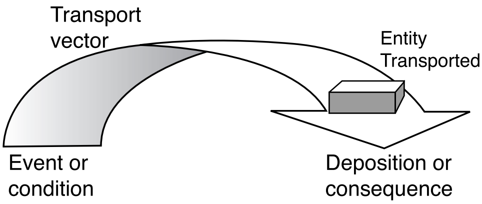

FIGURE 5.1. Diagram of the four components of propagation phenomena. Redrawn from Reiners and Driese (2004).

conveyance mechanism or vector operating through one or more media, (3) a conveyed entity, and (4) a locus of deposition or consequence (Figure 5.1) (Reiners and Driese 2001, 2003, 2004). There are analogies between ecologically relevant propagations and information transfer; indeed, some propagations primarily involve the transfer of information, such as the displays and sounds of many kinds of animals (Bradbury and Vehrencamp 1998). Propagations also involve transport of matter, such as slope-wash, or of energy, such as momentum of wind. Some, but not all, propagations are viewed as "fluxes" because with propagation, some quantity of an entity must move through some space or point at some rate. However, quantity and rate are not the essence of some propagations so that "flux" is too narrow as a general descriptor.

Initiating Events or Conditions

Events or conditions initiating propagation can range from spatially discrete and brief phenomena, such as the crack of a twig under a predator's paw, to something as large and pervasive as an earthquake resetting slope angles and stream grades. In fact, initiating causes can vary in at least seven distinct ways. Initiating causes (1) can be characterized by the kind of environment in which the events or conditions occur, (2) may be of abiotic or biotic origin, (3) can emanate from a natural process or an anthropogenic action, (4) may be discrete events or chronic conditions, (5) have a spatial extent, (6) can vary in duration of the action, if they are discrete events, and (7) may have a periodic character, if they are discrete phenomena.

Properties (4) through (7) in the list above are relativistic problems, requiring explicit definitions of the scalar context for the immediate case in question (Peterson and Parker 1998). Determining the origin of cause is, itself, relativistic as illustrated by the familiar *butterfly effect* (Gleick 1987). Definition of causation at a distal level, however, may be philosophically satisfying but mechanistically frustrating. It really is not useful to know that the stroke of a butterfly's wing will ultimately lead to a tornado in Topeka. It is more useful to seek causation at a more proximal level (*sensu* Robertson 1989) such as meteorological dynamics over the Central Plains.

The extent of the initiating cause should not be confused with the extent of environmental space that is impacted. The extent of crustal displacement along fault scarps related to earthquakes may only be centimeters to meters, but the extent of the earth's surface disturbed by these displacements may be thousands of square kilometers. Similarly, a chronic condition like an acid mine seep may occupy square meters, but its outflows may alter stream chemistry for many kilometers.

Entities

Propagations require that something be transported from the site of initiation to the locus of deposition (Figure 5.1). A neutral word for the item transported is *entity.* An initially simple approach is to classify entities into parcels of energy, matter, or information. Further thought reveals, however, that many entities one might consider to be energy also involve matter, such as the energy of atmospheric momentum. Likewise, many forms of matter bear with them some measure of energy, such as free energy of organic matter or reduced inorganic matter, or the momentum of transport itself. Finally, it may be neither the energy nor the material content itself but the information content that may impact the target destination. This is particularly true of biological targets. The transport of coded light signals generated by insects or fish, of programmed sounds such as mating calls of birds, or of genetic information bound in transported spores, pollen, and seeds are important from an informational point of view, not for incorporated energy and material content.

The definition of entities is dependent on their locus of deposition and on the point of view of the observer. Waves beating on the base of sea cliffs may be viewed as products of wind energy transformed to hydraulic energy eroding the cliff base through mechanical action. In this sense, the individual waves are energetic entities. But the waves also consist of water with dissolved and suspended substances, so that matter as well as energy is transported via wave motion. Whether waves moving onshore are material or energetic entities depends on the observer's phenomenological interest.

Vectors

Propagations require a transport mechanism to move entities from places of origin to loci of deposition (Figure 5.1). *Vector* is a term for any agent providing transmission of an entity across space (Weins 1992). As with initiating causes, an operational level has to be selected for determining vectors. It is possible to generalize broadly and attribute a multitude of vectors under the category of gravity (e.g., surface and groundwater flows, tides, and mass wasting events). Obviously, this level of causation does not provide much useful information. At the other extreme, we can describe vectors in utmost detail that extends to particular cases, such as exactly the kind of mass wasting process (e.g., Summerfield 1991). An intermediate position between most distal and most proximal definitions of causation underlying vectors is used in the following discussions.

Consequences

Eventually, transported entities are deposited, resulting in consequences somewhere in environmental space (Figure 5.1). Deposition may involve dissipation of heat, the triggering of an epidemic, absorption of sound waves, or the insertion of a new genetic variant. As emphasized earlier for causation and entities, definition depends on the viewpoint of the observer.

Propagations as Space-Time Phenomena

In some cases, it is acceptable and appropriate to view propagations at their terminus of action, or as instantaneous phenomena, so that their trajectories through time can be ignored. But, the fact that propagations take place over finite periods of time must be kept in mind. Propagations are both spatial and temporal phenomena (Kelmelis 1998; Reiners and Driese 2003, 2004). The areal or volumetric extent of the zone of deposition, impact, or consequence changes over time, whether it is the spatial extent of a snow avalanche rollout during the fractional seconds of its passing, the expanding seepage zone of a pollutant leak as its plume flows outward over days and years, or the nearly continuous flux of trade winds. Obviously, the spatial extent of a propagation is related to the viewer's temporal scale; the longer the time, the greater the extent in many, but not all, cases. Extended further, propagation time-awareness implies that heterogeneities in the environment, such as depressions and mounds found on forest floors left by tree tip-ups, are legacies of propagations past. Thus, a local environment, however defined, is a product of ongoing propagations of varying types, frequencies, periodicities, and intensities, as well as of propagations of the past.

How Transport Processes Are Affected by Environmental Heterogeneity

Effects of Heterogeneous Media on Propagation Initiation

Environmental heterogeneities not only influence the transport of entities but also may be the immediate initiators of propagations (Figure 5.2). A riverine flood plain meandering through a grass- or shrubland can be a sand source for dune systems that may stretch for hundreds of kilometers downwind of the flood plain (Knight 1994). Analogously, an acidic spring can alter stream chemistry for many kilometers downstream (Schnoor 1996). Initiations caused by heterogeneities may be probabilistic as well as

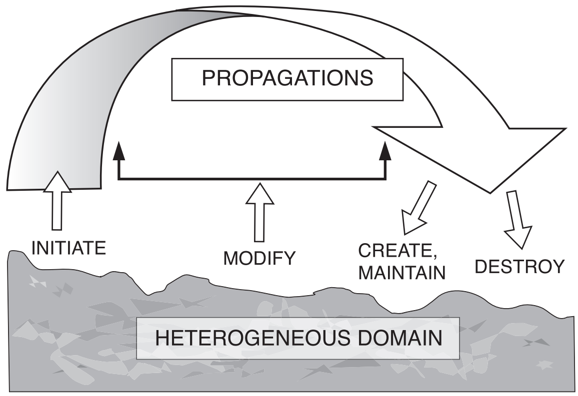

FIGURE 5.2. Diagrammatic relationships between environmental heterogeneities and propagations. Heterogeneities can initiate and very frequently modify the flow paths and intensities of propagations. Propagations, on the other hand, may be essential to create, maintain, or destroy environmental heterogeneities.

deterministic. There is a higher probability of lightning strikes on high ground than on low in terrain with relief. There is a higher probability of high nitrate fluxes from cultivated source areas than forested source areas on third-order watersheds (Herlihy et al. 1998).

Effects of Heterogeneous Media on Propagation Flow Paths

On a perfectly homogeneous and infinite plane or in a homogeneous volume, a physically driven propagation would move across the plane or through the volume simply as a function of the underlying physics of the driving vector. In fact, such perfect propagations rarely occur because of environmental heterogeneity. In a finite world composed of a layered atmosphere overlying continents of variable roughness interspersed, in turn, among oceans, the media through which propagations are transmitted vary in space and time. Further, media interfaces like the land-atmosphere interface or the sea-atmosphere interface modify transport processes. Although much transport modeling has concerned itself with ideal cases involving putatively homogeneous media, for ecologists, the more interesting cases involve cases featuring heterogeneous environments (Kelmelis 1998; Reiners and Driese 2001, 2004).

The influence of heterogeneity on transport processes obviously depends on the physics or biology of the entities and vectors involved. For example, molecular diffusion must move from areas of high concentration to low. Stronger effluxes of biogenic gases emanate from soils where the dog is buried. Of course, burying the dog was yet another propagation event, in this context an accident of history. Once initiated, diffusion rates will be pathway-controlled, as described in the example in the next section. It should be noted that the term *diffusion* is used here strictly in the physical sense of heat or molecular movement in response to concentration gradients. Diffusion is also used by others as an analogy for other dispersal processes, especially those occurring over extents of meters to kilometers, involving composite transport processes, or even cultural transfers (e.g., Banks 1994; Barrell and Pain 1999; Nakicenovic and Grubler 1991; Okubo and Levin 2001; Turchin 1998).

For all vectors driven by gravity, surface topography or variation in subsurface properties are the primary source of heterogeneity. Water, rocks, ice, and particles move downward in response to gravity in cases of transport by fluvial, colluvial, or glacial modes and with gravitational sedimentation. In both subaerial and submarine environments, flows tend to initiate at higher points in the topography, but then flow directions and flux fields are directed by topographic variability. For groundwater flows, the effective topography is subsurface variability in conductivity. To an extent, some currents are also gravity driven by either astronomical forces or by the earth's gravity on density gradients. Although it is ultimately true that tidal currents are initiated by gravitational pull of the sun, the moon, and other planets, the better explanation at a global level is that irregularities of the sea surface caused by these attractions lead to water running "downhill" from high areas to low on the oceanic surfaces (Mellor 1996; Pinet 1998). In this sense, topographically directed gravitational fields are both initiators and modifiers of fluid flows.

Both aquatic and marine nontidal currents and wind are ultimately derived from differential heating over space but are then directionally altered by Coreolis force, boundary constraints (bottom surfaces, islands and continental interfaces), surface roughness, and by density gradients established by temperature and salinity differences. Thus, at all scales, currents and wind are initiated, or powered by, environmental heterogeneities. Whether these causes are initiating or modifying factors depends on one's scale and vantage point. Nocturnal, downslope winds originate at high elevations and dissipate at low elevations. At the scale of a mountain-valley complex, an observer would describe such winds as differential air densities associated with altitude. At the scale of a mountain slope segment, an observer would contend that topography constrained the velocity and direction of the propagation.

Electromagnetic radiation, including all wavelengths occurring on the earth, encompasses radiation from the sun and the moon, from all substances on and in the earth, and biologically generated light (Bradbury and Vehrencamp 1998). Obviously, radiation originates from sources, sometimes diffuse, like the atmosphere; sometimes from specific points, as from a bacterial cell. Once emitted, radiation can be refracted at media interfaces, absorbed, scattered, or reflected by substances suspended in any translucent material. Some of these substances can be large, like plant leaves, producing complicated direct light environments (Endler 1993). These large and small objects then become elements of environmental heterogeneity for radiation transfer.

Sound is in many ways analogous with light and diffusion. Sound may come from extensive sources like surf along a beach or from highly concentrated sources like a rasping cicada. In either case, sources are discrete elements of environmental heterogeneity. Sound dispersal is then very much controlled by heterogeneities in the transporting medium like thermal layering in air and water or by reflective barriers like hills and sedimentary plumes in water.

There are many ways in which environmental heterogeneity underlies the initiating condition for transport by animal locomotion. Pollen transport by insects from plants in one wetland site to another or forage transformation of grass to feces could be initiated in an upland grazing site, then transported to, and deposited in, a lowland watering site. As Aldo Leopold observed years ago, animals tend to feed high and transport altered materials to low points on the landscape (Leopold 1949).

The previous paragraphs illustrate how many propagations are initiated and directionally modified by environmental heterogeneities. As with many things ecological, definition of initiation is scale-dependent. To say that the Gulf Stream is part of a global transport complex receiving its name from the Gulf of Mexico is true and useful from a global perspective, but for those living on Bermuda, the Gulf Stream is a continuous flux that controls local water and air temperature. Also, when one views propagations over time, the importance of differential stochasticity becomes apparent. Some insect outbreaks leading to out-migrations are more likely to occur in old-growth forest stands than younger stands in heterogeneous, forested environments (Holling 1987). Similarly, mass wasting events are more likely to occur on slopes oversteepened by lateral cutting by streams below than on slopes above aggrading portions of the flood plain. Fluvially transported nitrate is more likely to originate from agricultural fields than from forest plots on a multiple-use watershed (Herlihy et al. 1998). Depending on the entity and vector, it is possible to map the probability of initiation and subsequent flow direction based on patterns of relevant environmental heterogeneities.

How Propagations Produce and Destroy Environmental Heterogeneity

The Role of Propagations in Creating and Maintaining Environmental Heterogeneity

The foregoing sections have emphasized the influence of environmental heterogeneity on propagations, both in their initiation and modification. In fact, there is a marked reciprocity between propagations and environmental heterogeneities inasmuch as the latter are often generated by, and subsequently maintained, modified, or obliterated by transport processes. In fact, one could make an argument that all environmental heterogeneity is caused by propagations. To take the extreme case, two of the most common and dominant forms of heterogeneity—topography and surface geology—are created on one hand by tectonics and volcanism (mass movements of the earth's crust), and, on the other hand, by erosion and deposition by various forms of gravity- or wind-driven transport. Although this extreme case may be true, such a broad view will be set aside because it defeats the usefulness of considering propagations as an active part of nature on shorter timescales typically used by ecologists.

More practically, let us consider the kinds of heterogeneity found in the environment at less than the scale of landscape evolution. For the purpose of this discussion, we can divide heterogeneities into those that are anthropogenic, such as road networks and land-use patterns, and those that are products of more or less natural processes. The latter class includes oceanic currents, gyres, and eddies (Barber 1988); stream networks (Harmon and Doe 2001; Smith et al. 1997); intrastream bars and banks (Fisher and Welter 2004); dune systems (Yaalon 1982); forest gap mosaics (Bormann and Likens 1979; Pastor et al. 1998); fire patches (Romme 1982); and various kinds of linear, wave-like structures observed in oceans (Mellor 1996), lakes (Kratz et al. this volume), and on land (Billings 1969; Sprugel 1976; Klausmeier 1999; Hiemstra et al. 2002; Wu et al. 2000; Tongway and Ludwig 2004). Of course, there can be interesting interplay between human-caused *versus* naturally caused patterns—an interesting topic in itself.

Within this range of examples, it is difficult to discern a case in which transport processes at an ecological time frame are not involved in production or maintenance of patterns. However, there surely are such cases, and they must carefully be sought out (Butler et al. 2003). For example, it is possible that some of Watt's classic cases of pattern and process of tussock or clonal patterning are totally autogenic and independent of resource flows (Watt 1947). A careful review of the large number of cases of environmental heterogeneities would be necessary to characterize patterns of causation. Nevertheless, it seems that many heterogeneities are created by either episodic propagations like glacial advances and retreats, wind storms, fires (a special case of wind), and other large-scale extremes, or by the interactions between biological damage by propagated physical stressors and resource sequestration provided by material fluxes.

The latter class of heterogeneities, those caused by interactions between propagated stresses and resource fluxes, is of particular interest to ecologists because of the seemingly self-organizing nature of such patterns. Patterned heterogeneities of this type were first described by Watt (1947) under the title "pattern and process," the meaning of which is how pattern reveals, and is caused by, process. Pattern and process has since been described numerous times. It was reviewed by White in 1979 and by Turner in 1989 and is the dominant theme of a recent landscape ecology book (Turner et al. 2001). "Process" in pattern and process actually has dual meanings: the processes underlying construction and maintenance of the physical pattern (*sensu* Watts 1947), and collective processes resulting from the pattern (e.g., Schlesinger et al. 1996). In fact, causative processes on one hand, and resulting processes on the other, may be restatements of the same phenomena. That tussocks capture water, organic matter, and nutrients transported downslope by sheet-wash describes the concentration of resources and extraordinary plant growth in islands or stripes and explains the result—the existence of those plants. The coincidences of reproductive mode (or plant life span) and crucial lengths between resource collection areas *versus* accumulated stressors leading to plant demise and the existence of vegetated patches are just interesting details crucial to the local example (Ludwig et al. 2000). The principal point here is that these kinds of self-organizing phenomena often depend on transport processes, so that there is a constructive relationship between environmental heterogeneity and propagations.

The Role of Propagations in Destroying Environmental Heterogeneities

The intimate relationship between propagations and environmental heterogeneities is enhanced further by the fact that episodic propagations like tsunamis, hurricanes and tornadoes, ice storms, landslides, floods, fire, and lightning strikes also obliterate heterogeneities and possibly create new ones. If the intensity of a propagation event is sufficient and its footprint larger than the grain of the heterogeneous pattern, destruction of the antecedent heterogeneity, patterned or not, will result. Of course, a subsequent heterogeneity will then be established. Scaling relationships between destructive disturbances and heterogeneities probably exist for individual environments and episodic propagations characteristic of that environment. For example, there may be a scaling relationship between tree age and windstorm strength for a given vegetation type that will, most of the time, maintain a gap-phase mosaic but beyond which will occasionally destroy enough forest to eliminate the original, finer grained mosaic pattern (Foster et al. 1998).

Spatial Representation and Modeling Propagations

To this point, the discussion of propagations and heterogeneities has been general and abstract. What about measurement and prediction in realistic situations? How are propagations through spatially varying media and over irregular surfaces actually measured in nature? Examples are found in several environmental science disciplines such as geomorphology (earth surface processes), hydrology, atmospheric sciences, epidemiology, animal behavior, oceanic hydrodynamics, fire science, and aerobiology (Reiners and Driese 2004). In many, if not the majority of cases, propagations are estimated by scaling up from a few point measurements. Scaling up may be a simple statistical process, such as kriging, but it usually involves joining observations with representations of the spatial domain with or without a Geographic Information System (GIS) (Fischer 2000; Fotheringham 2000) through some kind of modeling. Large-scale examples are global circulation models that assist in weather forecasting. These are highly mature three-dimensional models operating in a spherical geometry and incorporating (assimilating) point measurements from around the globe to update climate dynamics in order to estimate fluxes of energy and matter throughout the atmosphere (Henderson-Sellers and McGuffie 1987).

Modeling propagations over and through heterogeneous environments introduces two kinds of issues. The first is about environmental representation with spatial data; the second about simulating transport processes themselves in variable environmental fields. Discussion of these vital, methodological topics goes beyond this paper. Portals to this voluminous literature are Longley et al. (1999, 2001), Clarke et al. (2000), Varma (2002), and Reiners and Driese (2004).

Producing Areal Estimates from Point Models of Flux Through Spatially Distributed Modeling

A commonly desired estimate is for vertical fluxes of energy or matter from sediment to water column, from water column to atmosphere, from atmosphere to soil, and so forth, extrapolated over a heterogeneous spatial domain. These are usually derived from point models (zero-order models), the outputs of which are varied according to heterogeneity of the spatial domain. Variation in the spatial domain can be represented in either vector (discretized map units based on aggregated environmental features) or raster (regular or irregular tessellations like rectangular raster) format (Burrough and McDonnell 1998). Outputs from all of the representative areas are then summed to give domain-level estimates of flux.

One assumption in such operations is that there are no lateral transfers between the representative areas within the time frame of the modeled phenomenon. If lateral fluxes do occur, they are parameterized or subsumed within site properties of the areas represented by the point models. For example, Reiners et al. (2002) estimated trace gas fluxes over a region using 1-ha cell rasters for six environmental variables. Lateral drainage transfers probably occur between the 1-ha cells but were assumed to be negligible over the time frame of the estimates (days to a year). Had the modeling time frame been extended to decades or centuries, estimates of lateral transfers between map units would have been required.

If some measure of variance with the estimated flux from the entire modeled domain is desired, it becomes necessary to account for covariance relationships for the multiple environmental drivers represented by multiple, overlain data sets. In fact, this is rarely done. In the same example cited above (Reiners et al. 2002), some of the spatially distributed data, such as soil texture, had statistical distributions rather than singly determined, categorical values (e.g., landcover type for each raster cell). Iterated model runs using random values drawn from these distributions served to produce replications of output from which means and variances, including covariances, could be calculated. Means from cohorts (tuples) covering the domain were added, and variances pooled, to gain summations of regional, vertical propagation with estimates of variance properly incorporating covariance. Regional estimates were also calculated with the typical method of simply summing singly determined values for cohorts. This latter, more commonly used method led to an underestimate of 8% for one gas and 18% for another.

Modeling Propagations Moving Laterally Across Heterogeneous Environmental Fields

Perhaps more interesting are lateral propagations across heterogeneous environments. As wind blows across, or animals move through, terrain with variable vegetation cover, environmental heterogeneity influences the transport process itself. In other words, there are explicit interactions between points on the domain. These cases require two-dimensional spatial modeling, and in some cases, demand three-dimensional approaches. Two-dimensional modeling can involve vertically oriented as well as horizontally oriented planes. Glacial movement and oceanic currents are frequently modeled as vertical, two-dimensional planes (Holland 1986; Mellor 1996; Konrad et al. 1999). Of course, vertical plane, two-dimensional modeling can be combined with representations of environmental variation on orthogonal, horizontal planes to produce a pseudo-three-dimensional system. Two examples follow in a later section. Others are reviewed in Reiners and Driese (2004).

Modeling Three-Dimensional Processes in Two Dimensions

Although most propagation phenomena are actually three-dimensional in physical character, many, if not most, are treated in two dimensions. This is managed by parameterizing the third dimension as functions of features represented in the two-dimensional map units. For example, transport by wind involves eddy formation and turbulent transfer between the atmosphere and land and water surface. These interactions are three-dimensional but are "flattened" to two dimensions by parameterizing roughness length and effective surface element height for the two-dimensional plane (Garratt 1992). Similarly, subsurface flows in hydrology models are handled in two dimensions by parameterizing estimated porosities and saturation values of watershed spatial units (Beven 2001).

What is lost by flattening propagation processes to two dimensions? Depending on the objectives, this flattening may be perfectly acceptable. In fact, given all the additional data, modeling and computations needed to treat explicitly the third dimension, a two-dimensional approach may be the more intelligent one. As with admonitions about using the proper data structure and scale, however, it is essential that investigators be aware that adoption of widely used practices may be inadequate for the question being addressed. If, for example, dry deposition to various layers of a three-dimensional forest canopy must be known, a three-dimensional approach is necessary. Similarly, if detailed subsurface conditions in the hyporheic zone are essential to predicting biogeochemical processes (Hedin et al. 1998; Hill et al. 1998; Schindler and Krabbenhoft 1998; Fisher and Welter, this volume), and these must be known over a horizontally variable domain, then three-dimensional modeling will be necessary.

Three-Dimensional Modeling

It would seem that true, three-dimensional propagation modeling would be important to ecology. The foraging of martens on the ground and up trees, the spatially distributed deposition of nitric oxide within forest canopies, the changing redox state of soil aggregates with rainfall events, are all important phenomena that might best be dealt with in three-dimensional framework. There has been little development in this area in ecology, partially because of the enormous computational and parameterization demands of three-dimensional modeling, but also because of the lack of conventional software packages equivalent to GIS. Some of the conceptual potentials and problems in this area are reviewed by Couclelis (1999), Rogowski and Goyne (2002), and Peuquet (2002). More such work has been done in climate modeling, groundwater pollution, and oil and gas exploration and "production." Three-dimensional vector and voxel (cubic "pixels") methods are both available in these fields, and ecologists might be advised to investigate these possibilities for appropriate ecological problems.

Yet another technological frontier is the addition of the fourth dimension—time—to these problems. Ecologists usually regard nature in four dimensions, and the time will come when they will want to model in four dimensions as well. For thoughtful treatments on four-dimensional representations, see chapters in Egenhofer and Golledge (1998) and Longely et al. (1999).

Three Examples of Propagation Modeling in Heterogeneous Environments

To better describe how propagations are modeled for heterogeneous environments, this section demonstrates how three vectors have been modeled to incorporate environmental heterogeneity (from Reiners and Driese

2004). The three examples are wind transport, molecular diffusion, and animal locomotion. Particular attention is paid to choice of environmental variables incorporated into the environmental representation, choice of environmental data structure, extent of modeling domain, modeling grain size, time steps used, how three-dimensional processes were handled, and the data platform and modeling languages typically used.

Wind Transport

Wind is the motion of air relative to objects. It is one of the more pervasive transport vectors in the environment and features high variability in its direction and velocity. Wind entrains, transports, and deposits sensible heat, latent heat, hydrometeors, gases, and aerosols. Aerosols include condensation products of atmospheric chemistry, soot, soil dust, salt spray, hydrometeors, and biological products. Biological aerosols include detritus, pollen, spores, seeds, fruits, and living invertebrates (Isard and Gage 2001). The relative importance of wind transport in environmental space varies locally depending on source strengths, wind trajectories and velocities, and surface properties (Reiners and Driese 2004).

A model for transport of snow by wind was adapted by Reiners and Driese (2004) from Hiemstra et al. (2002) for treeline in the Medicine Bow Mountains, WY. This model was adapted, in turn, from Liston and Sturm (1998). Static (in the time frame of the model operation) spatial data over the domain—the elements of environmental heterogeneity—are elevation, slope and aspect, patches of trees and krummholz, and the snow-holding capacity of vegetation types (Figure 5.3A). Temporally varying inputs—other aspects of environmental heterogeneity—include wind speed and direction, precipitation rate, temperature, and humidity. Model mechanics are based on calculated wind velocity at the surface and on the shear strength of the snow. All spatial data are represented in a 5-m rectangular raster. The entrainment, transport, and deposition of snow are parameterized with respect to topography and boundary layer surfaces. Thus, the third dimension is parameterized in terms of the surface plane so that this is a pseudo-three-dimensional model distributed over a two-dimensional surface. (See Figure 5.3B for results of one model run.) This example shows how a pseudo-three-dimensional approach is adequate for propagation processes in which the flux or deposition is expressed in terms of area.

Molecular Diffusion

Diffusion is used here in the original sense of heat and mass transfer by the movement of molecules, or very small particles, due to their kinetic energy (Harris 1979; Monteith and Unsworth 1995). This is in contrast to the usage of diffusion described above as a default model for complex phenomena that are difficult to parameterize at the scale of the actual processes (e.g.,

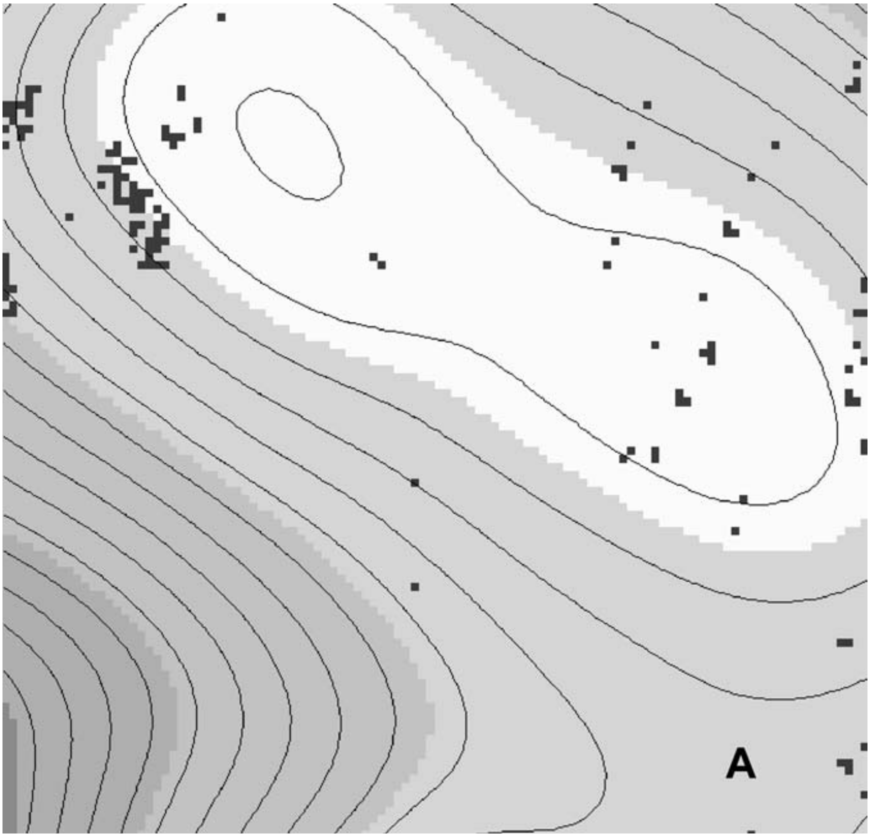

FIGURE 5.3. (A) Topography and tree vegetation of the Libby Flats treeline area of the Medicine Bow Mountains, WY. The area is 500 × 500 m in extent, and the elevation ranges from 3224 to 3239 m. Lighter shades are associated with higher elevations. Elevation contours are in black, and the areas occupied by trees are represented as dark pixels. (B) Modeled snow depths with darker shades indicating more snow. Black contours are elevation; white contours are snow depth. Snow depth ranges from 51 to 121 cm. Higher, windward (wind flows from left to right) locations tend to have less snow; positions leeward of topographic highs and trees tend to have more snow.

Pastor et al. 1998; Turchin 1998; Choy and Reible 2000; Hemond and Fechner-Levy 2000; Okubo and Levin 2001). Molecular diffusion involves transport lengths of only millimeters to centimeters but occurs over enormous surface areas ranging from the aggregate surface areas of bacterial cell walls to the ocean-atmosphere interface.

Reiners and Driese (2004) modified SNOWDIFF, a model originally formulated to simulate one-dimensional gas diffusion from soil through the snow pack to the atmosphere at one place on the landscape (Massman et al. 1997), to a two-dimensional mode. Diffusion is based on Fick's law with the

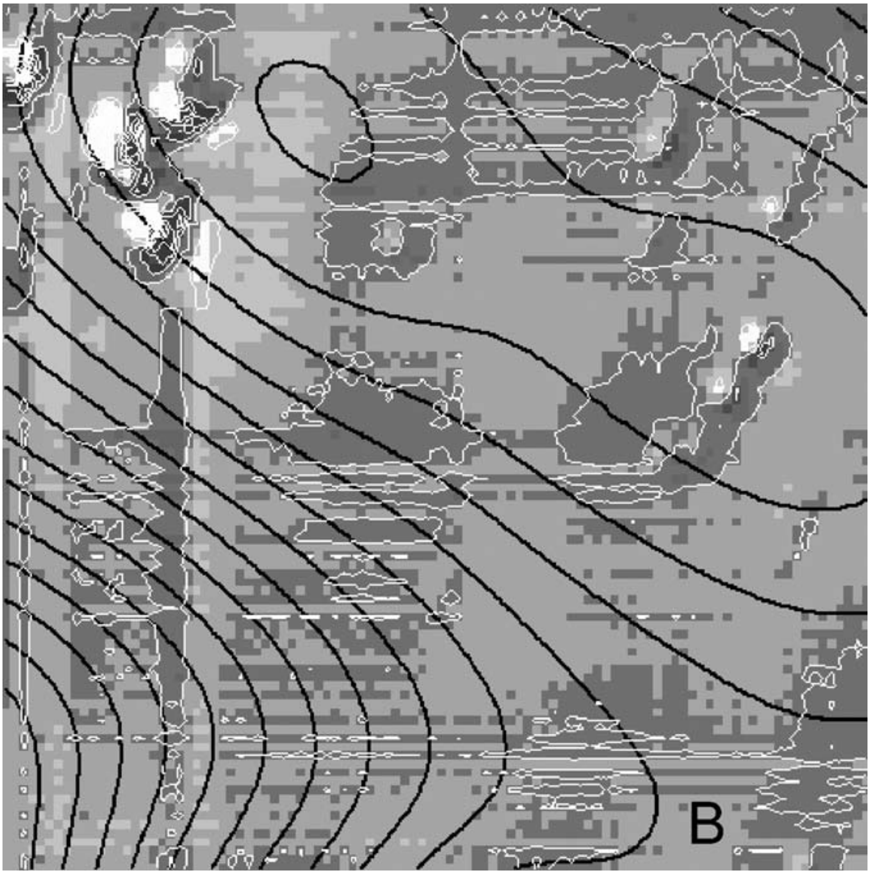

FIGURE 5.3. (*Continued*)

concentration gradient based on measured soil and atmosphere concentrations and resistances estimated from individual layers by thickness, porosity, tortuosity, and temperature. Environmental variables used in the point model—the elements of environmental heterogeneity—are snow depth and porosity by layers. There is no estimate of lateral diffusion between points (cells). CO_2 diffusion is extrapolated over the same 500 × 500 m treeline domain described previously for the wind model by running the model for each 5-m cell in a raster representation of landscape for which snow properties are known. Because flux is entirely a property of diffusion of gas through snow and largely controlled by snow depth, estimates of gas flux (Figure 5.4) are very similar to estimates of snow depth (Figure 5.3B). This is actually a one-dimensional model run repeatedly over a two-dimensional grid of snow profile properties to estimate a vertical flux in a pseudo-three-dimensional space without lateral transport.

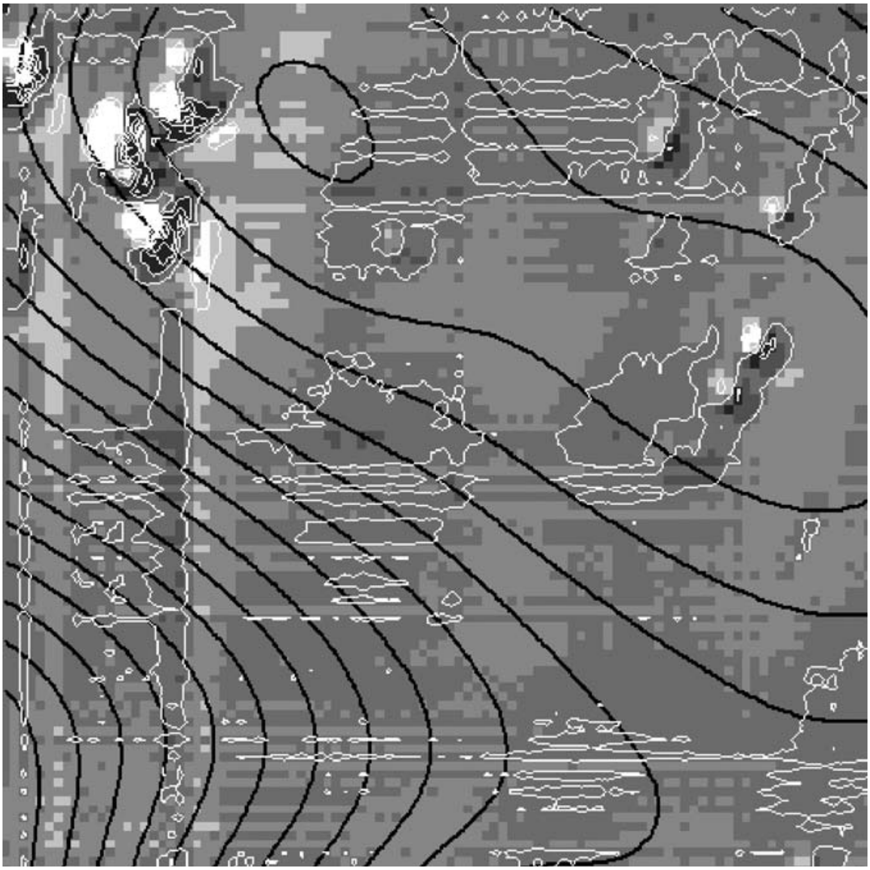

FIGURE 5.4. CO_2 efflux rates as a function of snow distribution (Figure 5.3B) resulting, in turn, from factors represented in Figure 5.3A. Black contours represent elevation; white contours indicate snow depth (see legend for Figure 5.3B). Lighter shades indicate higher CO_2 flux rates. Flux rates in this model output range from 3.9 to 9.1 Mg m^{-2} s^{-1}.

Animal Locomotion

Locomotion is found in some stage of all members of the earth's biota but is particularly marked in animals and protists. As animals disperse, forage, flee, and mate, they move through environmental space—both aquatic and terrestrial, fluid and solid. In their movement, animals act as vectors by transporting their own biomass and leaving a trail of their influences, whether it is foraged materials, mechanical alterations of the medium, or exuvia.

Reiners and Driese (2004) produced a pine marten movement model to illustrate how some simple rules and environmental representations could lead to movements similar to those recorded in the field. The landscape

FIGURE 5.5. Map of simulated pine marten travel trajectory in a heterogeneous Rocky Mountain subalpine environment. The dark black patch in the center of the figure is a lake, a habitat type that is crossed quickly due to exposure to predators. The dark gray is the best habitat, medium gray is moderate quality, and light gray is poorest quality habitat. The line trace indicates 500 simulated movements of 5 m each.

configuration is based on actual U.S. Forest Service land cover data for an area of 1 × 1 km in the Medicine Bow National Forest. It is a two-dimensional vector-based representation of three levels of habitat suitability (high, medium, and low), plus water (Figure 5.5). In this case, environmental heterogeneity is represented as relatively large polygons relative to scale of animal movement. Rules for marten behavior were derived from observations on tracks in the snow. These were converted to probabilities of martens crossing habitat boundaries and turning angles made in transit through the environment as functions of the habitat type. Field data showed that angles were more acute in favorable habitat and obtuse in unfavorable habitat like water. Animal location and movement in the model is vector-based in the two-dimensional environment represented by the vector habitat layer (Figure 5.5). For heuristic purposes, users can vary turning angles associated with habitat types, number of time steps, and distance traveled per time step. This example illustrates how individual animal movement modeling may be done and subsequently coupled with animal impacts such as predation or habitat alteration.

How Might a Propagation Perspective Influence Our Conceptualization of Nature and Ecology?

How we individually create mental frameworks for environmental heterogeneity and propagations is conditioned by our personal experiences, our intellectual predilections toward what we see, and our methods for representing nature. This is as true in natural science as it is in philosophy, religion, and art. The ways that ecologists view a landscape or seascape are influenced by what they know and how they individually represent nature based on their personal and disciplinary experiences. Interviews with several ecologists examining a common scene can reveal disparate "visions" of the scene. Some ecologists instinctively seize upon common color or textural "blocks" in the landscape (patch mosaic or patch matrix) as a means of mentally organizing variation in the domain in question regardless of what the eyes see. Others force a landscape image into raster cells similar to a remotely sensed image by ignoring unifying elements (continuous variation). Some ecologists will "see" environmental gradients, whereas others will "see" the imprints of historical events. Some see clues of ongoing change, whereas others see static patterns. Outside of ecology, many atmospheric scientists and oceanographers "see" their realms in terms of wave spectra. Our environmental cognitions vary in surprising ways and to considerable degrees.

How might a sense of flows and movements in all their variety influence our views of nature? Combined with sensitivity for heterogeneity at all scales, how would this alter our views of the environment? In the extreme, we might envisage the world as composed of temporary structures having more or less heterogeneity at given scales and bathed in a range of flows of variable intermittency and influence that alternatively create and destroy the heterogeneous features. Such a vision would return ecology to the spatial and geographic science that it once was.

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