

RESEARCH PLAN

A. Background

Ecosystems are the meeting grounds upon and within which species interact with each other, and with their physical and chemical environment; they are integrated networks of biotic and abiotic elements through which materials and information flow, and that support our continued existence on the planet. From ecosystems we derive food and fiber, fuel and pharmaceuticals. Furthermore, they mediate local and regional climates, stabilize soils, purify water and in general provide a nearly endless list of services essential to life as we know it [1]. The case for the preservation of ecosystems and these services is manifestly clear, but the essential challenge of how to do it depends on our knowledge of [2] how macroscopic properties develop from, and feed back upon, diverse assemblages of biotic and abiotic elements. This is unquestionably the essence of understanding biocomplexity—how it arises, and how it is maintained [3].

At the levels of ecosystems, as well as the biosphere as a whole, macroscopic features and processes such as nutrient cycles, nutrient limitation, hydrological dynamics, resiliency, stability, and structural diversity emerge from the complex interplay of myriad biotic and abiotic elements. Such emergent properties define the ecosystems themselves, and provide the contexts within which species interact and evolve. As such, they are fundamental to the persistence of plant and animal populations, and to the preservation of the services humans derive from natural systems. Some of the patterns that emerge are unique to particular environments, but others—such as ratios of nutrients—show remarkable regularity within wide classes of systems. We will address both the similarities and the differences. Our first goal will be to identify those generic features that are common to many ecosystems, and to explain why they are constant across environments. Complementary to this, we will characterize differences across systems, especially those that arise through marine-terrestrial comparisons, and seek explanation of the observed distinctions. Most crucially, we will ask how observed patterns arise and are maintained in the face of and as a result of competitive interactions and natural selection acting at levels far below that of whole systems. Our focus will be on the interplay between biotic evolution and the cycling of nutrients, trace elements and water, and how system resiliency is maintained in changing environments.

The existence of broad cross-systems patterns—such as the Redfield ratios of nutrients in dissolved inorganic nutrient pools in the oceans, or similar ratios in terrestrial systems—poses a fundamental paradox: How do extraordinarily constant patterns emerge at the ecosystem scale, from the tremendous (and evolving) biotic and abiotic complexity that characterizes natural ecosystems? In this proposal we integrate empirical observations and theoretical models to address key aspects of this paradox. Specifically, we shall investigate both the reasons for the regularities that are observed, and equally the reasons that such regularities may not hold across all systems. That is, we will ask how macroscopic patterns emerge from local interactions, and how cross-system differences, such as mixing patterns, can account for differences in observed properties. This will require the development of theoretical approaches to allow exploration of the ecological and evolutionary interactions among individuals, species, environments and nutrient cycles, at a variety of scales of organization. Our basic approach will be to develop ecosystem models that couple the behaviors of individuals with ecosystem processes operating at much more aggregated levels. In this way, we can examine evolutionary patterns and trends by allowing for the infusion of novel genotypes and characterizing the resultant ecosystem self-organization, including changes in the capacity of the system to tolerate novel stresses. A specific focus will be an examination of the role of the very different rates of mixing in marine versus terrestrial environments in accounting for differences in observed patterns.

The research will be solidly grounded in empirical observations, through the work of Hedin in terrestrial systems, and Morel and Ward in marine systems. Levin, Pacala and

Durrett have extensive expertise in ecological and evolutionary modeling, and will be responsible for development of the terrestrial models, and for cross-system comparisons. Flierl and Grünbaum have worked for many years with Levin on individual-based models of marine systems, and will be responsible for the modeling of movement patterns in marine systems, and for integrating marine physics and biology. Rodriguez-Iturbe is an expert on hydrology, and especially on the self-organization of hydrological cycles. He will be responsible for this component of the research, and for integrating hydrology and biology in terrestrial systems.

B. Key issues

The first point of attack for our research will be understanding what determines element ratios in marine and terrestrial systems, and why there are differences across systems. Alfred Redfield noted as early as 1934 that, despite the prodigious diversity of species and life strategies in the world's oceans, nitrogen (N) and phosphorus (P) are maintained in extraordinarily constant concentration ratios in both seawater (at least in the upper layers) and biomass [4-8]. Analogously, despite the wealth of life history and nutritional strategies that have evolved among terrestrial organisms, primary production in forests is N-limited in most temperate regions, but appears to shift predictably from N- to P-limitation during tropical forest development [9-11]

A major focus will be on the role of mixing. Marine and terrestrial systems operate on very different temporal and spatial scales, with the oceans showing much higher mixing rates across local environments. Furthermore, mixing is evolutionary labile; and in the oceans and on land alike, mixing rates vary by orders of magnitude among species. Thus it will be essential not only to allow for this diversity, but also to examine how dispersal and mixing rates evolve within communities of interacting species [12].

It is further paradoxical that the available information shows that forest ecosystems also develop towards a constancy of N:P ratios in ecosystem outputs, but that these differ by orders of magnitude from the oceanic Redfield ratios [11]. Water is also a limiting resource on land, and its cycling and availability are inextricably linked to nutrient cycles; in forests local organism-water interactions may set limits to primary productivity and nutrient losses at the ecosystem scale. Thus we will treat macronutrients, trace elements and water as part of an integrated system, examining how patterns of resource availability coevolve with life histories.

The existence of macroscopic properties at scales of entire ocean basins and forested regions is relevant both for basic questions on how biocomplexity emerges above the organismal and species level, and for applied questions about sustainability and management of ecological systems. Despite this broad theoretical and applied importance, major uncertainties remain in our understanding of how macroscopic properties emerge, and are maintained, within ecosystems. A key question is whether (and how) evolution acts to shape such broad patterns and, conversely, how local evolutionary processes are influenced by feedbacks between macroscopic and microscopic processes. Consider the difficulties inherent in understanding how local organism-nutrient interactions are linked to ecosystem-level nutrient cycles. Molecular scale processes operate at time scales of seconds, become integrated into the dynamics of individuals, and from there to populations. While populations and species compete locally for nutrients over ecological time scales [e.g., 13, 14, 15] it is more difficult to understand how such interactions influence, and are influenced by, the long-term (years to millennia) changes in inputs, outputs, and recycling of nutrients that are manifested at scales of entire ecosystems [e.g., 10, 16, 17] and ultimately the cycling of atmospheric gases. And yet, these multiple organizational scales are inextricably linked: While populations and communities control the proximate cycling and retention of nutrients in local environments, macroscopic nutrient cycles provide the ultimate context within which all organism-nutrient interactions are embedded and evolve over time.

C. The central role of natural selection

Ecosystem patterns and processes emerge from the interplay among adaptive processes at multiple levels of integration—from the evolutionary processes that operate at the level of organisms, to the dynamics of interactions at much higher levels. Ecosystems and the biosphere change over ecological and evolutionary time, largely as a consequence of selection operating upon their component parts [18]. Emergent properties that affect the functioning of entire ecosystems can feed back over longer time scales to influence microevolutionary processes in a dynamic and evolving manner. Other properties are little more than the consequences of scaling up from local laws, providing allometric fractal-like patterns that may or may not be consequential [19]. We will examine both. To do so addresses the compelling need to integrate processes at levels of individuals and ecosystems. Evolutionary models naturally focus on the population consequences of differential fitnesses of individuals within their biotic and abiotic contexts, but must thereby explicitly consider feedbacks that arise from evolution at the more aggregated levels of populations, communities, and entire ecosystems. Conversely, ecosystem-scale models must be made more mechanistic through explicit consideration of how individual organisms and their traits contribute to the emergence of macroscopic properties, and the role of evolution in reshaping the distribution of traits within ecosystems. Such integration across organizational levels will naturally generate questions about the principles that guide the self-assembly of communities into networks of species and genotypes that can resist invasion by novel strategies. What are the impacts of interannual hydrologic fluctuations in the organization of these communities? How stable are they to invasion?

Efforts to integrate natural selection with theories of ecosystem scale phenomena too often have foundered on the shoals of group-selectionist arguments. For example, biosphere processes that are fundamental to our life support systems may appear to have been shaped by evolution for such purposes—a form of homeostasis by and for the biosphere [20]. Such arguments have become increasingly prevalent, given current interest in what maintains global systems, and are closely related to theories that seek to explain ecosystem patterns in nutrient cycling, resiliency and diversity in terms of their benefits to the systems as a whole. These notions, however, do not sit well with evolutionary biologists, who understand that evolutionary forces operate primarily at much lower levels of organization; hence, they regard group-selective arguments as anathema. There are, indeed, feedbacks from the macroscopic to the microscopic; but these are diffuse, and operate over long time scales. Recognition of this has led to the development of the Daisyworld class of models [21, 22]; but these are metaphors, not tied closely to particular systems.

A second central issue for understanding the development and maintenance of ecosystem patterns at evolutionary time scales is the question of whether macroscopic system properties are sensitive to the evolution of novel traits and strategies. Of particular concern are strategies that can potentially act to de-stabilize homeostatic properties. Notable examples include the evolution of oxygenic photosynthesis on Earth, which resulted in dramatic shifts in the earth's atmosphere, in redox conditions, and in the subsequent evolution of metabolic processes on earth. It is possible to imagine analogous effects on ecosystem properties caused by the evolution of species capable of fixing atmospheric N_2 , of symbiotic mycorrhizal associations, or of changing underlying physiological constraints regarding relative nutrient requirements.

Attention to this problem, stimulated especially by Lovelock's seminal and provocative writings [20, 23], has tended to focus on homeostatic mechanisms at the broadest scales. In this research, we propose instead to direct attention to some striking regularities that exist at the ecosystem level, in order to produce a theory that can be tested against data across a range of ecosystem types. Research at the level of the biosphere is complicated by the fact that we have only a single realization, with a single historical context. By focusing on ecosystems, we can consider the effects of environmental conditions, and sort out the relative roles of extrinsic and intrinsic factors in the self-organization of biological communities and ecosystems.

THE FUNDAMENTAL QUESTIONS

Motivated by the general considerations developed in the preceding section, we propose to address a set of five specific questions:

- A. Why do constant element ratios often develop at macroscopic scales, despite the heterogeneity of environmental conditions (such as patterns of productivity and the great biotic diversity at local scales), and how are they sustained in the face of continual evolutionary change over longer time scales?
- B. Why do macroscopic element ratios differ so dramatically between marine and terrestrial ecosystems? What environmental differences, such as extrinsically-determined mixing patterns, are most responsible for observed differences?
- C. How are nutrient cycles in ecosystems buffered against evolutionary invasion by novel strategies, and in the face of nonlinear interactions and possible regime shifts over ecological time?
- D. Under what conditions do properties such as ecosystem resiliency and stability increase over ecological and evolutionary time scales, and when are these features lost? How different are the patterns that emerge in complex adaptive ecosystems, in which evolutionary forces are strongest at the level of individual agents, in comparison with what would be expected were systems being optimized for functioning as integrated units?
- E. What scaling rules emerge for system-level properties, for example involving biotic/geochemical/hydrological interactions? To what extent do these resolve the paradoxes mentioned in the earlier questions? How do these emergent allometries feed back to influence natural selection at lower levels?

Our approach will be to characterize the patterns of interest at the macroscopic level, and then to explore developmental alternatives through coupled ecological and evolutionary models that allow microscopic innovation, while producing macroscopic patterns that can be tested against observations.

A. Nutrient patterns in marine and terrestrial systems

In 1934 Alfred Redfield noted the extraordinary constancy of the ratio of the concentrations of nitrate and phosphate in seawater and its similarity to the N:P ratio in the suspended biomass. Sixty-six years later, with a lot more data at our disposal, this observation still stands. And it is even more surprising now than it was then, for we have learned that the rates of gain and loss of fixed nitrogen (denitrification and nitrogen fixation) in seawater are much higher than heretofore suspected and seemingly controlled by factors unrelated to each other. There are deviations, especially for short periods or in regions with strong N limitation [24], or at great depths [25]; but these do not change the general picture. We also know that a remarkably constant Redfield type ratio approximately applies to other bioactive elements, such as essential trace metals [26].

In discussing his observations, Redfield noted that they lead to a classical chicken-and-egg argument: Seawater resembles the biomass because organisms control the geochemical cycle of bioactive elements; the biomass resembles seawater because organisms have adapted to the available elements in seawater. Clearly these sorts of arguments beg for a more fundamental constraint. It does not appear that biochemistry provides it, since various organisms in environments can exhibit widely different elemental composition and physiological uptake requirements [27]. In fact, a recent and puzzling observation is that aggregated ecosystem models predict that the Redfield ratio is highly sensitive to any physiological change in N and P requirements among algae [7, 28]. In addition, the wide diversity in nutritional strategies among species raises the long-standing "paradox of plankton" [29]—why a diversity of species can coexist in a well-mixed environment, and in the apparent face of extraordinary constancy in N:P ratios in space and time. Geochemistry alone certainly would not lead to the observed elemental ratios, since at least the nitrogen cycle is biologically controlled. Similarly, biology—separated from

geochemical processes—would not lead to the observed constancy of ratios, given the propensity for evolutionary change of organismal physiologies and nutritional strategies. It thus appears that the explanation for the observed Redfield ratios in seawater lies in the interplay between geochemistry and biology, between global element cycles and biological adaptation and competition. This interplay is also presumably responsible for the paradoxical fact that nitrogen (which can be fixed by the biota) rather than P (which cannot) is typically observed to be the principal limiting nutrient in marine waters.

In terrestrial systems, the phenomenon of nutrient limitation is often seen as emerging from short-term interactions between supplies and demands of nutrients in local environments [e.g., 13, 14, 15]. However, such localized organism-nutrient interactions depend upon, and are embedded within, inputs, losses, and recycling of nutrients at the scale of entire ecosystems—processes that develop over periods of years to millennia and that are crucially dependent on interannual climatic and hydrologic fluctuations [e.g., 10, 17]. Efforts towards a comprehensive theory of how organism-nutrient interactions develop and evolve within ecosystems must therefore consider links between processes that operate at very different spatial, temporal and organizational scales.

Despite the importance of Redfield ratios for our understanding of ocean nutrient cycles, analogous studies of terrestrial ecosystems are rare. Some efforts have considered nutrient ratios of different plant and soil pools [e.g., 30, 31], or variations in tissue nutrient ratios within and among tree species [e.g., 32]. However, there have been few attempts to explore whether forested ecosystems develop characteristic nutrient ratios at the whole-ecosystem scale. Our own work on ecosystem nutrient losses in deep soil waters (collected by lysimeters below the depth of root turnover, estimated from ^{14}C depth profiles), and in small watershed streams [17], suggests that—indeed—such diagnostic ratios may emerge over long periods of ecosystem development. Since hydrologic nutrient losses reflect the integrated sum of organism-nutrient interactions in a forest ecosystem, hydrologic loss ratios of nutrients can be taken as analogous to Redfield dissolved nutrient ratios.

Our studies of unpolluted tropical forests in the Hawaiian Islands show that hydrologic losses of total N and P equilibrate at ratios that are > 30 times higher than Redfield's diagnostic ocean ratios [11]. This N:P ratio appears to emerge within 20,000 years of ecosystem development (based on studies of 6 sites along a geometric soil age gradient from 200 to 4.5×10^6 years; described in Crews et al. [33] and Chadwick [10]). The loss ratio remains between 27-35 times higher than the Redfield ratio for all study sites older than 2,000 years. In contrast, our studies of three unpolluted temperate forest watersheds on old and non-glaciated soils in southern Chile show the maintenance of lower total N to P loss ratios over five years of study: ca. 6-9 times the marine Redfield ratio. Roughly similar ratios (ca. 9-14 times Redfield) have been reported from a few studies of European and North American forests [34, 35], but may be confounded by histories of glaciation as well as industrial pollution. Collectively, these ratios are broadly consistent with the idea that temperate forests are primarily N-limited, while older tropical forests display P-limitation of primary production [11, 36]. More importantly, the results raise two questions that are fundamental to this proposal: Why do macroscopic nutrient ratios appear to differ so dramatically between marine and terrestrial ecosystems, and so dramatically between temperate and tropical forests?

We will address these questions by assembling broader empirical data sets on N:P ratios within and among different forest ecosystems, and by comparing these empirical patterns against those produced by the modeling efforts described below.

B. Conceptual limitations of current models

Models of ecosystem nutrient cycles (e.g., century, TEM, etc.) have traditionally focussed on functional aggregates of organisms (primary producers, decomposers, etc.) that compete for nutrients made available in spatially homogenous and well-mixed pools. These models have emphasized nutrient cycles at the ecosystem scale, and generally paid less

attention to implications of individual organism-nutrient interactions, of environmental structure, and of variations in the availability of nutrients. An important consequence of all these aggregated models is the prediction that, in the absence of frequent disturbance events, ecosystem nutrient cycles develop towards a dynamic equilibrium among inputs, outputs, and internal recycling for any nutrient. However, this prediction has been difficult to reconcile with population-scale theories on nutrient limitation, since it predicts that nutrient limitation is only an ephemeral phenomenon during the development of ecosystems. In fact, a wealth of empirical studies show that nutrient limitation is both a common and persistent property of aquatic and terrestrial ecosystems.

It has recently been suggested that this "standard ecosystem model" is sensitive to changes in several key assumptions, and may fail to capture important classes of interactions. For example, Hedin et al. [17] and Vitousek et al. [37] have illustrated that the inclusion of biologically unavailable forms of nutrients among ecosystem output vectors provides a mechanism for the indefinite maintenance of nutrient limitation at the ecosystem scale. Such losses of unavailable nutrient forms are in fact common in natural ecosystems, as chemically complex forms of dissolved organic N or P lost via deep soil water in terrestrial ecosystems [see 17], or as fecal pellets and particles that sediment out of the mixed layer in aquatic ecosystems [24, 38]. Others have suggested that the standard model can be sensitive to individual organism-nutrient interactions [39, 40]. In this case, differences in nutrient ratios between resources and consumers (e.g., algae and zooplankton) are thought to control how nutrient limitation and nutrient cycling develops at the ecosystem-scale. If such local organism-nutrient interactions are included, together with variations in organismal strategies of nutrient acquisition, the standard model becomes sensitive also to differences in spatial structure and rates of mixing of local environments. For example, a process such as N fixation may be favored in local environments, even if it would not be globally favored under the standard assumption of homogeneous and fully mixed ecosystem pools [11].

We here propose to build a different set of nutrient cycling models. Our models will be based on spatially explicit interactions between organisms and nutrients, and will allow for differences in nutrient availability, in organismal strategies of nutrient acquisition, and in rates and spatial extents of environmental mixing. Hydrologic dynamics will play an important role in these phenomena. By allowing organismal traits to be heritable, and by including mechanisms of resource competition, our models will incorporate the processes of natural selection at the level of individuals. Most broadly, we seek to understand how macroscopic patterns of nutrient cycling emerge from interactions of different organismal strategies, from feedbacks across organizational levels, and from evolutionary changes that occur at the scale of individuals. We are particularly interested in understanding the emergence of complexity, and the development of (and limits to) internally generated properties such as self-regulation and resiliency.

C. Space and the evolution of individual characters

Novel traits arise as localized deviations from a norm, and spread (or do not) initially as a result of local interactions. The explicit spatial structure of the environment, therefore, is of essential importance in understanding the evolution of basic traits; indeed, evolution of life-history traits such as dispersal and dormancy affects the scales at which a genome samples the environment, and hence those scales themselves respond to selection.

Different traits and strategies define classes of organism-nutrient interactions in natural ecosystems, with consequences for how macroscopic properties differ between terrestrial and aquatic ecosystems. In forests, attributes such as nutritional strategies, dispersal, growth in high- vs. low-light environments, and shading are all fundamentally intertwined with the spatial structure and relative lack of mixing of the system. Whereas competition for nutrients, moisture, and light, are forms of exploitation competition, other strategies include interference competition, and the beneficial (or neutral) exchange of nutrients

between different species. For example, shading emerges as an interference strategy, evolved to benefit its owner by reducing the effectiveness of a competitor. In contrast, associations between plants and mycorrhizal fungi (or N_2 fixing bacteria) emerge from benefits associated with reciprocal transfers of carbon and nutrients. Spatial structure is central to the evolution and persistence of both strategies: vertical attenuation of sunlight in the case of shading, and predictable contact between organisms (in space and time) in the case of beneficial associations. Moreover, these strategies can markedly affect macroscopic ecosystem patterns [41-43], as long as interactions are locally sustainable and not subject to invasion by competitors or cheaters.

Allelochemicals provide another mechanism of interference competition. Allelopathy, in which organisms produce chemicals that poison competitors, is a well-documented form of competition among plants [44], as well as among bacteria [45]. The evolution of allelopathy is fundamentally dependent upon the degree of mixing. For bacteria, for example, Chao and Levin found that they could not select for allelopathy in well-mixed environments, but could do so when organisms were allowed to plate out on an agar gel. Varying the degree of mixing in spatial models produces the identical result [46-48]. The explanation is that, in a well-mixed environment, the benefits of producing allelochemicals are diffused, and hence the payback is not sufficient to overcome the metabolic costs of producing them. Furthermore, the benefits are not restricted to those producing the chemicals, but are shared alike by evolutionary "cheaters" that develop resistance, but do not produce the poison.

Despite higher mixing rates, however, local interactions in marine systems are also important for the evolution of adaptive traits. Thus, the model of selfish behavior just discussed has relevance to the evolution of many of these, such as chelation. Over the past few years, it has become apparent that most trace metals that are essential to the growth of aquatic microorganisms—Fe, Zn, Cu, Co, Ni, Cd—are complexed by strong organic chelating agents in surface seawater. This chelation decreases the inorganic concentration of the metals to extremely low levels and reduces greatly their availability to microalgae. While we do not know the exact nature of most of the chelating agents, we know that they are of microbial origin and, in the case of iron, that at least some of these are siderophores—chelators produced by bacteria for uptake via specific Fe-siderophore transporters. This extracellular chelation cannot accelerate the rate of Fe uptake—uptake of inorganic Fe is more effective than that of chelated Fe—but it greatly reduces the availability of Fe to other organisms, which must either make do with very low inorganic Fe or extract it from the chelator via reduction. Thus chelation (at least of Fe and probably also of Co) seems to be a strategy of monopoly: various microbes release binding agents that make the metal available only to themselves [49].

The first paradox is that of ecological stability of such a system: how could it be stable against cheaters? We know there are cheaters and some bacteria synthesize cross-membrane transporters specific for iron chelators that they do not themselves produce. In view of the immense cost associated with modifying trace metal chemistry in very dilute seawater, it would seem that the organisms that synthesize and release siderophores would be quickly outcompeted by such cheaters. We therefore need explicit spatial models to explore the diffusive dissipation of benefits and to identify the conditions under which strategies such as chelation can evolve. The second paradox comes from a striking inverse proportionality between the inorganic concentrations of metals in seawater and their rate constants for coordination with ligands; these rate constants depend chiefly on the rate of detachment of the coordinated water in the first hydration sphere of the metal ions [50]. Since marine microorganisms can apparently take up trace metals as fast as reaction kinetics permit, it seems that all metals may be effectively taken up at the same rate (within a factor of 5 or so) in surface seawater. This inference is corroborated by the observation that the cellular concentrations of various essential metals in marine phytoplankton are within a factor of 5 of each other. For example, the concentration of cellular iron (which is necessary for myriad biochemical functions) is only two to five times that of cellular Ni or Co (each of

which has very few known biological functions in eukaryotes). What interplay of adaptation, competition and biogeochemical cycling leads to such a surprising result?

The above examples illustrate the need for models that link organismal strategies and ecosystem-scale properties and feedbacks. In addition, these models can be used to examine the sensitivity of local interactions, and macroscopic patterns, to invasion by cheaters or competing organismal strategies.

METHOD OF APPROACH

Motivated by the considerations of the earlier sections and the within- and across-ecosystem patterns described, we will use individual-based models of terrestrial and marine systems to pursue the following particular goals. We will set out to address a number of specific questions:

1. Investigate the basis for the regularities seen in the Redfield ratios of the oceans. How and why do these ratios differ between terrestrial and marine systems? What are the spatial and temporal scales of nutrient limitation?
2. More generally, elucidate the role of mixing (and the relative absence of it) in explaining the differences observed across systems, and specifically the evolution of strategies of cooperation and competition among species.
3. Examine in what ways the patterns observed in ecological systems differ from what might be expected, for example maximum productivity, if ecosystem functioning were optimized at the systems level, rather than emerging from evolutionary processes operating at lower levels of organization.

The dynamics of ecosystems emerge from the collective dynamics of huge numbers of individual parts, and in turn feed back to influence those parts. We need, in effect, to build a statistical mechanics of ecological communities, founded upon a combination of observation, controlled experimentation, simulation and mathematical theory.

Ecological communities are not entities constructed *de novo*, by a developmental process akin to the ontogeny of an individual organism. They have not been shaped through natural selection for their macroscopic properties, as have been organisms, because they are not reproduced as units that faithfully replicate genetic material. Rather, they are complex adaptive systems [18], whose collective properties emerge from interactions and a process of selection operating at myriad levels of organization below the whole system. Ecosystems are loosely defined assemblages of interacting elements, exhibiting structure and functioning at almost every scale of organization, and interchanging genetic material so freely with other ecosystems that they cannot represent evolutionary units. That is not to say that they do not evolve—they do. But that evolution is more the result of the evolution of its component species, weakly interacting across multiple scales of space and time, rather than the evolution of coherent entities in the classical Darwinian sense.

A. Development of models

Our general approach will be to develop individual-based models of terrestrial and marine systems, in which factors such as mixing and organismal traits can be easily controlled. We will explore both the self-organization of systems over ecological time, and their evolutionary dynamics. In the latter case, this will necessitate introducing new types through mutation and other mechanisms, and using and extending modern methods of studying evolutionary dynamics [12].

Because the questions in this proposal cover a broad range, we shall employ a series of ecosystem models, each designed to address a different issue. However, the models are all special cases or variants of a general ecosystem model, which we outline here.

1. State variables

The environment in the general model consists of a collection of spatial cells indexed by the subscript “ x ”. Cells in models of terrestrial forests will usually cover the area of the crown of a single adult tree, but will sometimes be considerably larger. Each cell will include not only the space above ground, but also the undecomposed organic matter and mineral nutrients below ground. Initially, we will treat the soil within a cell as homogeneous, and so will not explicitly model the effects of depth on biogeochemical transformations. Ultimately, we will allow for two depths—a shallow one with labile organic matter (which turns over at annual scales, like leaves) and a deeper one with more resistant soil organic matter (which turns over at decadal scales, like soil). Cells in models of oceanic ecosystems will include the euphotic zone (surface waters) within an area small enough to be considered homogeneous. The appropriate size and mixing rates for these cells will be a topic of explicit research using the equations of fluid dynamics. In particular, we will use the methods derived in Flierl et al. [51] to derive mixing rates and grid-based (Eulerian) descriptions from individual-based (Eulerian ones).

Each cell will contain three kinds of entities. First, individual autotrophs will be represented as vectors of the inorganic resources (i.e. carbon, nitrogen, phosphorus) contained within their bodies. Let $b_{ijkx}(t)$ be the amount of resource k contained in individual i of type j in cell x . The different types of autotrophs will be different species in some applications and different genotypes in others. We designate $B_x(t)$ as the set of the $b_{ijkx}(t)$ for the cell. In what follows we omit the time dependence of all state variables to simplify the notation. Also, in many applications of the approach, individuals will have type-specific stoichiometric (nutrient) ratios of resources, and so we will need to keep track only of individual biomass (designated b_{ix}). Moreover, in several applications, cells will contain

many individuals, and we will track only the total biomass of each type in the cell: $\sum_i b_{ijkx}$

Cells will also contain resources in a variety of non-living organic and inorganic forms. Let R_x be the set of non-living resources in cell x . Each element of R_x gives the total amount of the resource (r_{kwx}) of type k in state w . Here, type designates chemical element (nitrogen, phosphorus etc.) and state covers anything that affects availability, loss, or mineralization, including alternative inorganic forms (i.e. nitrate vs. ammonium), the ease of decomposition of dead organic matter in which the resource is bound, and whether or not the resource is complexed with a chelating agent. Again, we will not attempt to include all of this complexity at once. A typical application will involve a single resource in two states (say chelated and unchelated), or a few different resources, each in a single state.

Finally, in some applications, cells will contain compounds that affect the vital rates of living organisms or biogeochemical transformations without being nutrients per se. Examples include water in terrestrial systems, allelopathic compounds, chelating agents, and carbohydrate root exudates. Let the vector C_x represent the abundance of these chemicals in cell x .

2. Movement, inputs and outputs

Cells will gain and lose materials in up to three ways (see Figure 1). First, living organisms will leave their cell and/or export nutrient, seeds or larvae at rate m (sessile organisms, of course, will effect dispersal only by the latter mechanism; that is, through their propagules). Dispersing individuals will be equally likely to move to any cell in the metapopulation although movement rates will vary among types. A similar rule will govern transport of R_x and C_x to other cells. We will consider initially the extremes of uniform global mixing among cells, and nearest-neighbor movement; but ultimately, intermediate cases will be important [52]. In oceanic applications, movements of phytoplankton and dead material will occur at rates that are coupled by physical transport. In most terrestrial applications, only

seeds will be exchanged among cells. Second, depending on the application, atmospheric inputs of wind blown dust, chemical weathering, nitrogen fixation, and/or rainfall may add directly to specific nutrients of B_x , R_x and C_x from outside the system, whereas leaching in terrestrial systems, evaporation, volatilization, denitrification and/or runoff may remove materials from the system. Third, in models of oceanic ecosystems, material that sinks from the surface waters represented by the cells will enter a single well-mixed pool representing deep subsurface waters. This common pool will have its own vector of R and/or C . Upwelling will return substances from the common pool to the cells of the surface zone, and material in the common pool may be received from outside the system and lost to the outside by sedimentation and weathering. Note that we could transform the system smoothly from an oceanic to a terrestrial pattern of nutrient cycling by simultaneously reducing rates of upwelling toward values consistent with terrestrial weathering, decreasing the sinking rates toward values for terrestrial leaching, increasing the losses from the common pool to the outside (toward infinity), and altering the cell-to-cell mixing. This may prove useful to understand some of the fundamental differences between oceanic and terrestrial ecosystems.

In marine systems, for dealing with higher trophic levels, we will also explore a complementary approach, as developed by us [51] for exploring patterns of aggregation. Planktonic systems are patchy at almost every scale of investigation; major contributions to that patchiness include the predator-prey interactions between individuals [53] and the active movement of individuals in response not only to environmental cues, but especially other individuals. Since this means that grid-based movement rates will be density- and frequency-dependent, it is essential to derive these from Eulerian translations of individual-based (Lagrangian) models, which capture the evolutionary strategies of individual in the ways they respond to their abiotic and biotic environments. We [51] have been investigating methods for doing this for more than a decade, and Flierl et al. [51] provides recipes for addressing all of the situations of interest in this proposal.

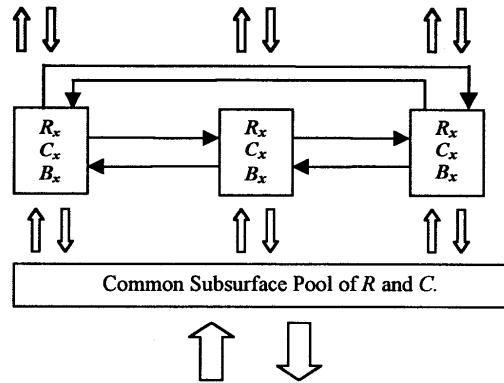


Figure 1

4. Plant vital rates, nutritional strategies, and biogeochemical transformations

To complete the model, we require type-specific vital rates for the living organisms and rates of biological production, decay and biogeochemical transformation for the elements of R and C . For simplicity, we will typically use the simplest of formulations for rates of death, seed or larval production per unit biomass and resource losses in litter or dendrites per unit of living resource, by making these constant across of species, genotypes and resources. Growth rates will be plant type specific and, in the most general case, will depend on the state of an individual organism (b_{ijx} , the vector of values b_{ijkx}), and the other organisms, resources and chemicals in the cell. We label $G_{jk}(b_{ijkx}, B_x, R_x, C_x)$ as the rate of increase of b_{ijkx} , and thus the rate of uptake of resource k by individual i of plant type j in cell x . We assume that organisms take resources and deposit materials only within their

own cell. The chemical forms of dead plant tissue and other additions to R_x and C_x by plants will also depend on plant type in some terrestrial applications, so that we may study the development and control of leaching rates, mineralization, and chelation.

Biogeochemical transformations convert resources from one form to another (e.g. from r_{kwx} to r_{kzx}). In most applications, one form of each resource will be available for uptake by plants, and the others will have different rates at which they are converted into the available form. The exception is that chelating agents operate the opposite way, transforming the available form into a form that only some organism types can use. We will introduce species with nutritional strategies that include exploitation and interference competition and between-species associations of varying benefits (positive to neutral) and symmetry (fully symmetrical to asymmetrical), and that permit species to gain access to external nutrient pools (e.g., N_2 fixers) or to promote losses of specific nutrients. In addition, we will in some cases allow species to have heritable variation in optimal nutrient ratios, while in other cases we will keep nutrient ratios fixed.

As an example, to investigate the puzzle of the constant Redfield ratio in seawater, our student, Lee Worden, has already used the general framework described above to model two (or more) biochemically necessary trace metals, r_{1wx}, r_{2wx} , and two (or more) species of autotrophs, $b_{1x} = \frac{b_{i1x}}{i}$, $b_{2x} = \frac{b_{i2x}}{i}$. Making the assumption that the trace metals r_k are taken up at differing rates, and that the population growth rates of species b_j depend on their ability to collect these metals from the surrounding water, we can flesh out the model into a system of differential equations in a straightforward way (space does not permit a full discussion here). Preliminary work on this system shows a strong tendency for these two species to reach a dynamic equilibrium in which, exactly as observed in the field, the external concentrations of these metals are maintained in inverse proportion to their uptake rates so that their effective uptake rates are identical.

With this general framework in hand, we will explore not only the ecological dynamics, but also the fundamental issues of evolutionary dynamics and stability. Communities will be assembled and modified through the continual introduction of individuals with novel traits, such as those described in the earlier sections of this proposal. The methodology for characterizing evolutionary stable strategies and more subtle variants on them have been well-worked out for the analysis of individual strategies [54]. Only recently, however, has attention been turned to how the theory of adaptive dynamics might be modified to address the coevolution of species within a community context [e.g., 12, 55]. To date, no efforts that we know of have integrated these with higher-level processes such as nutrient dynamics. This will be a primary goal of our analysis.

B. Assembly of empirical data sets

We will link these modeling efforts with the construction of new data sets on nutrient contents and ratios in terrestrial and aquatic ecosystems. Because of the sparse to nonexistent information from terrestrial ecosystems, we will emphasize the assembly of data sets on broad patterns of nutrient ratios in forest solution losses, and in plant and soil pools. We will use two sources: 1) data already published in the literature, or from Hedin's collaborations in Chile and Hawaii [11, 17], and 2) collection of new data from > 70 watersheds throughout southern Chile, for which we presently have only incomplete measures of nutrient losses [56]. A postdoctoral associate will assemble these databases, and ensure that the resulting empirical patterns are dynamically integrated with the numerical models.

HYDROLOGICAL AND FLUID DYNAMICAL INFLUENCES

To this point, we have examined the ecological and evolutionary emergence of ecosystems under given and homogeneous environmental conditions. In both terrestrial and marine environments, however, heterogeneity is important. Furthermore, and especially in terrestrial systems, environmental heterogeneity codevelops with ecological complexity.

In this section, we ask

1. To what extent are patterns in the distribution of the biota determined by, or at least correlated with, patterns in hydrological or fluid dynamical factors?
2. To what extent can macroscopic patterns in hydrology (and, indirectly, of vegetation) be derived from locally-defined physically-based principles?

In marine and terrestrial systems alike, it is crucial to understand how the physics of flows may influence or even control ecological patterns and processes, including biotic use (through productivity) or losses of nutrients through leaching in terrestrial systems.

The spatial and temporal scaling observed in different systems and processes in hydrology (e.g., river basin structure, rainfall occurrence and amount of precipitation, etc.) and in oceanic mixing patterns is likely to have a signature in the space-time structure of ecosystems. This structure spans a wide range of temporal and spatial scales, which are frequently linked through power laws valid for the description of a large number of ecosystem characteristics, at least across some ranges of scales. The lack of intrinsic scales in power law probability functions is in itself a signature of scaling phenomena, and a major challenge in the near future will be to discover general types of dynamical syntheses that may be responsible for such signatures in space and time, and to determine how ecological feedbacks may modify the simple power laws. For example, marine zooplankton patchiness may be explained on the broadest scales in terms of fluid dynamics, and on smaller scales by the active movements of individuals in response to each other [51, 57].

Ecosystems are open dissipative systems with a large number of elements operating under highly non-linear conditions. Their exchange of matter and energy with the environment is frequently controlled by hydrologic and fluid dynamic processes and influenced by variables such as soil moisture and evapotranspiration, temperature or salinity. These are in turn crucially affected by ecosystem characteristics. In some cases, the scaling observed in time and space could result from self-organized dynamics where global behavior and structural coherence arise through local rules of interaction. The scale of the system of study is typically somewhat arbitrary, and it is crucial to understand how system properties scale with system size. In terrestrial systems hydrologic dynamics will be crucially important in the elucidation of the above local rules, especially for ecosystems where water is a controlling resource. It is necessary to clarify which are the most relevant and general of the scaling characteristics of ecosystems. How are these characteristics related to the water and energy exchanges between the ecosystem and the environment? For terrestrial systems, is there a linkage between the scaling observed in hydrologic processes and systems and the dynamics operating in different types of ecosystems? For marine systems, how do planktonic patterns of distribution correlate with temperature and salinity patterns?

A central issue [3] is to determine the extent to which patterns are determined by extrinsic factors, and the degree to which they are self-organized. Soil moisture and precipitation present clear signatures of spatial scaling, reflected among other things in the distribution of "islands" above a fixed level. Thus, if one intersects with a plane the spatial field of cumulative rainfall over a region without strong orographic effects, the resulting "islands" represent the areas where cumulative rainfall-say over a season-is above the preassigned level. A similar interpretation captures the "islands" of the soil moisture field. The probability distribution of the size of these "islands" has been shown to be a power law over many scales of area sizes [58, 59]. We plan to search for this type of scaling signature in the spatial organization of vegetation. Thus with the very detailed data now available for

several regions of the world we plan to study the distribution of cluster sizes for trees of different species under different types of climatic conditions. Do power laws apply over some scales; and if so, how do the exponents compare with these for soil moisture and cumulative rainfall? How does climate affect the exponents? Using measurements of basal area of individual trees over extended areas, we plan to build 2-dimensional fields of biomass over regions on different climates. We will then study the distribution of sizes of “islands” on the terrain where the biomass of a species is above a certain level.

We also plan to carry out an analysis comparing the distribution of biomass in forests with that found in dendritic structures in different natural systems. Very interesting for our purposes is the distribution of drainage areas in river basins. Thus the probability distribution of the area draining throughout a randomly chosen point in a drainage network is a power law with exponent of 0.43-0.45 over a large number of log-scales in sizes. This has been corroborated over many river basins throughout the world and is consistent with principles of minimum energy expenditure. Optimal channel networks (OCNs) derived from such principles reproduce extremely well this and other types of scaling signatures found in natural watersheds [19]. When OCNs are built with competition for space among different river basins the same types of power laws are observed. Figure 2 shows an example of these multiple outlet OCNs. These self-organized fluvial networks play a role analogous to the fluid dynamical forcing functions in marine systems, and the cascades of turbulence that redistribute materials to the oceans. Elsewhere [60, 61] we have initiated parallel analysis for marine systems

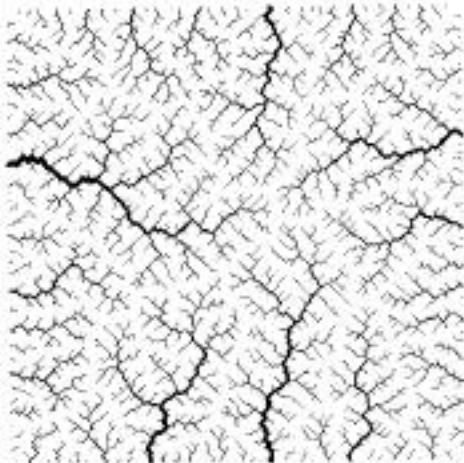


Figure 2. Multiple outlet OCN (from [19])

SPECIFIC RESEARCH AGENDA

As discussed in the earlier parts of the proposal, the main objectives of this research will be to relate population biology and ecosystems science, with explicit consideration of how individual-based interactions lead, over ecological and evolutionary time, to homeostasis in nutrient cycling, and in particular to the maintenance of element ratios at the levels that are observed. To address these questions, we have separated our work into three broad tasks:

- 1. Establishing the patterns observed in Nature, and the degree to which those patterns are determined by underlying physical and chemical features of the environment.*** For marine systems, there are well-known regularities in the ratios of macronutrient and trace metal concentrations, even though these may not be as regular as once assumed. Our preliminary work [11] indicates that the patterns in terrestrial systems are dramatically different. In the first stage of our work, Hedin (with a postdoctoral fellow)

will extend existing data sets, and develop syntheses that will provide a suitable complement to the marine generalizations. In marine systems, patchiness in the distribution of the plankton is observed on virtually every scale of investigation. Comparisons with the distribution of temperature and salinity suggest that on the broadest scales, this patchiness can be explained by fluid dynamical factors, while on the broadest scales the patterns are self-organized [60, 62]. We, led by Rodriguez-Iturbe, will conduct similar analyses for terrestrial systems, seeking to discover the influence of hydrological scaling laws on the distribution of vegetation.

2. Determining how communities become assembled over ecological time scales, and how coevolution shapes the roles of species within ecosystems.

Our basic approach here will be a collaborative effort to develop and analyze spatially explicit individual-based models such as those presented in Method of Approach section. Modeling of terrestrial systems will be led by Pacala and Hedin, with major input from Levin and Rodriguez-Iturbe. Durrett, with Levin and a graduate student, will develop and analyze reduced dimensional representations, building on his expertise in interacting particle systems. Modeling of marine systems will be led by Levin and Morel, with major input from Ward, Pacala, Flierl and Grünbaum. In particular, Flierl and Grünbaum will develop explicit Lagrangian approaches to the movement of individuals, and will use these to derive Eulerian descriptions that will facilitate marine-terrestrial comparisons. The analysis of the models will focus first on asymptotic behavior, in particular regarding the attainment of constant nutrient ratios. In order to understand the influence of extrinsic factors (such as climate), we will study the dependence of the asymptotic behavior upon those factors. We also will examine in great detail the role of mixing regimes, allowing for a range of dispersal and mixing within the ecosystem. We also will complement the ecological investigations through examination of evolutionary dynamics. In this work, following the techniques explored in [12, 55], we will develop an adaptive dynamics of ecosystems by allowing evolutionary innovation subject to constraints. Specific attention will be on dispersal, growth and competitive ability, on the tradeoffs among them, and on determining what determines biotic diversity within ecosystems. We also will examine in this phase the evolution of chelation, shading and allelopathy, as well as cooperative strategies. The modeling work will involve all participants, and will rely heavily on graduate students and postdoctoral fellows.

3. Determining the relationship between system structure and resiliency, and whether evolutionary forces increase or decrease resiliency.

In this phase, led by Levin, Pacala and Rodriguez-Iturbe, the models developed earlier will be used to examine the resiliency of systems to ecological and evolutionary perturbations, including climate change, loss of biodiversity, habitat modification and the introduction of novel genotypes. We will examine not only asymptotic behavior, but transients as well, to investigate whether ecosystems gain or lose resiliency during their self-organization. A particular focus will be the determination of the ability of systems to maintain their structure in the face of cheaters. We know that the localization of spatial interactions will play a fundamental role, and hence we will give this aspect particular attention both for terrestrial and marine systems. We also will explore the potential for systems to be shifted from one dynamical domain to a fundamentally different one, through multiplicative noise and other influences.

EDUCATIONAL ACTIVITIES

Graduate students and postdoctoral fellows are an integral part of this project, and about the majority of the funds requested are for their support. At Cornell, a postdoctoral fellow will work closely with Hedin on the assembly of empirical databases on terrestrial nutrient levels. This person will also be a key link to the modeling, and hence should have strong quantitative skills. Two graduate students at Cornell will also be involved with the modeling and evolutionary analyses, and will provide a link between Hedin and Durrett.

At Princeton, two graduate students and two postdoctoral fellows will be involved, and will provide a core interactive group, to be housed together (though also to have space in their home departments). All will be involved with some aspects of the modeling, but will have varying responsibilities in terms of model development and analysis. We have considerable experience with collaborative modeling of this kind, most recently through the Carbon Modeling Consortium, and find that it represents a highly productive research and educational environment.

Although no funds are being sought specifically for undergraduate students, Princeton is an institution in which undergraduate education and research plays a central role. We fully expect to involve students, especially seniors developing their senior theses, in aspects of literature review and analysis, as well as modeling. Having the core group of graduate students and postdocs will provide a highly stimulating intellectual environment that is certain to attract, and be supportive of undergraduates. Because of budget limitations in this proposal, we intend to seek support for undergraduate research experiences through other mechanisms, but are certain that these will be a central part of the project.

A. Outreach and dissemination

The proposed activity will be housed within the Princeton Environmental Institute (PEI), directed by François Morel (and formerly by Simon Levin). PEI involves more than 50 Princeton faculty, plus 3 who are on PEI faculty lines and whose teaching in part is mandated to meet PEI needs. Because those 3 are Morel, Rodriguez-Iturbe and Ward, and because Pacala and Morel are directors of PEI's 2 largest research centers (The Carbon Modeling Consortium and The Center for Environmental BioInorganic Chemistry (CEBIC)), the proposed project will immediately become a core activity of PEI and benefit from its structure. A principal mission of PEI, besides promoting interdisciplinary environmental research and teaching programs at Princeton, is to provide a conduit between Princeton and the public in order to make the results of Princeton scholarly research available and useful outside of academia. This particular mission entails organizing outreach activities that are directed at school children (K-12), at private and public leaders, and at the general public. We will participate fully in several existing activities aimed at enhancing science education, which include a summer teacher-training program, public lectures, and a science kit program.

During the 1998-99 academic year, PEI developed a new initiative to provide Princeton faculty and students with more opportunities to participate in environmental projects outside the University, and to engage the public in University-centered activities. These new outreach programs are designed to assist local school districts in their efforts to reform K-12 science education. PEI convened a series of organizational meetings, in conjunction with the Princeton Materials Institute (PMI), for local school district administrators and PEI/PMI faculty early in the year. Those meetings included not only a discussion of the science education reform effort, both nationally and locally, but also workshops involving faculty from PEI, related to the science kits discussed in the next section.

1. Scientific Kit Program

The Invention Factory Science Center, a new and innovative science museum in nearby Trenton, New Jersey, assembles and provides science kits for local K-6 teachers on subjects

such as air and weather, insects, solids and liquids, and ecosystems for its "Science to Go!" program. These kits are designed to provide teachers with the materials and support they need to teach inquiry-based science. PEI provides resources to support the kits, such as scientists available to respond to questions or to visit the classroom, enhancement materials, field trips and other assistance. The topics of our research should be especially attractive for this program, and project faculty will be available to participate fully.

2. Summer Science Institutes for Teachers

Princeton's Teacher Preparation Program runs a very successful "Quest" summer workshop for local teachers in grades K-12. Teachers come to campus for three weeks during the summer and are trained by Princeton faculty members and other local scientists in "hands-on" science projects. They receive a stipend and follow-up training throughout the school year. The lectures and projects that our instructors will contribute to this program will introduce the notion that the biosphere is an evolving system, and that it is essential to recognize its nature as a complex adaptive system if we are to manage it effectively.

PEI also holds training workshops during the academic year with Teacher Preparation Program, including one last year on "Exploring Environmental Science Kits," for approximately 30 elementary school teachers who have participated in Princeton's Quest summer workshops. PEI associated faculty, including François Morel and Steve Pacala, participated in this, and we would build upon and expand our involvement for the proposed project.

Last year, PEI partnered with the Woodrow Wilson National Fellowship Foundation in a summer environmental institute for over 50 middle and high school teachers from across the nation. PEI faculty provided lectures on the science behind global change, and postdoctoral fellows led small groups in hands-on lab demonstrations and modeling techniques. This activity will be continued in future years, and would be substantially enhanced through this research effort.

3. Outreach to the general public

In addition to the activities described above, the project will be able to take advantage of conferences and workshops that PEI organizes every year, bringing together leaders from academia, industry, public interest groups, and government. PEI also publishes a quarterly newsletter that is widely distributed to Princeton faculty, students, staff and alumni, and to members of government, industry, public interest groups, foundations, and universities. The activities of this research will be featured in such future meetings and newsletters, thus providing a means to publicize them beyond academia.

MANAGEMENT PLAN

Princeton will be the lead institution, and the bulk of the work will be done there. Hedin spent a sabbatical at Princeton developing the ideas in this proposal, and a very tight connection has developed among the various principal investigators. Durrett, Flierl and Grünbaum all have long histories of collaboration with Levin, including periods spent visiting Princeton, and effective collaboration at a distance.

As described in the last section, Hedin and Rodriguez-Iturbe will be responsible for data analysis in terrestrial systems, and the search for patterns and scaling laws coupling the physical and chemical environment with the biotic community. Morel, Ward and Levin will fulfill the analogous roles for marine systems.

Modeling will be led by Pacala (terrestrial systems), Rodriguez-Iturbe (hydrology) and Levin (marine systems), with major roles being played by all participants. In particular, Durrett will develop interacting particle system models that capture the essential features of the more complicated models, including efforts to represent physical flow regimes. Flierl and Grünbaum will be responsible for the development of Lagrangian models of marine systems, and for developing Eulerian translations that will facilitate marine-terrestrial comparisons. Hedin, Morel and Ward will be involved in all aspects of model development, in order to improve the biological grounding of assumptions.

The graduate student and postdoctoral fellow at Cornell will be supervised by Durrett and Hedin, and will be integral parts of the research. At Princeton, it is expected that the 2 graduate students and 2 postdoctoral fellows will be housed together, in space provided by the Princeton Environmental Institute (directed by Morel), and will form a truly interactive and integrating core group. However each will have 2 formal supervisors, drawn from the 4 PIs and Ward. Specific pairings will shift over the course of the grant, as tasks evolve.

The primary research will be done by investigators in their home institutions, but travel for frequent meetings will be crucial. In particular, Hedin and Grünbaum will make extended visits to Princeton (for as long as a month in the case of Grünbaum), and Durrett and Flierl will make shorter visits. There will be reciprocal visits, especially by Levin, postdocs and graduate students, to Cornell and MIT. Graduate students and postdoctoral fellows, in order to facilitate their integrative roles, will also spend time at the partner institutions.

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