

## PROJECT DESCRIPTION

### INTRODUCTION

The goal of this research is to develop and test the analytical tools needed to understand and predict the interactions and feedbacks among humans and aquatic species across complex landscapes. Our central organizing principle is that landscape patterns and changes in network structure and function are explained by energy and time optimizations of water flows, biota and humans. Although we understand many ways that each subsystem individually optimizes time and/or energy, each optimization imposes constraints on related subsystems, which can then change the rules by which each operates. Through these multiple feedbacks and interactions, even individually well-understood subsystems can produce unpredictable dynamics. Thus, we propose an integrated modeling framework to incorporate feedback and interactions among biotic and abiotic systems so as to accurately predict the effects of interactions of human and aquatic populations. These multiple feedbacks and resulting emergent properties are hallmarks of a complex adaptive system that can be simulated using an individual- (agent) based simulation model.

Typically, adding more complexity increases the variance and uncertainty of modeling predictions. **Our main overarching hypothesis is that an integrated individual-based model will more accurately predict environmental effects than any single physical, biotic or social model by reducing unexplained variation.** The mechanism generating this reduction in variance results from including cross-disciplinary connections and corresponding agent feedbacks to what otherwise would be missing in the individual disciplinary models (*e.g.*, human use as an explanatory variable in biotic systems). In order to test this hypothesis we will develop an integrated individual-based model of physical, biotic and social networks using energy and time optimization as a unifying principle with multiple feedbacks between networks as a framework to capture different hierarchical levels of complexity. In our case study, river and road intersections bring about interaction of natural and social agents, with mutual feedbacks (Figure 1). Dynamic interactions are captured by interdependent functions of each individual agent and each subsystem (*e.g.*, nearest neighbor dynamic). Thus, our approach integrates multidisciplinary field studies into a unified individual-based model that addresses fundamental problems of biocomplexity to quantify and evaluate different dimensions of interacting human and natural systems. The model will be developed and applied to test our main hypothesis along a land use continuum from coastal commercial, residential, agricultural and forested reserves. The experimental design relies upon an existing natural continuum in the level of road densities and road types within a network structure that reflects a hierarchy of land uses, geomorphic and riverine features. As detailed below, we will test the accuracy of predictions using all categories of interacting agents versus predictions based on sequential removal of one class of agents.

We hypothesize that there is an inverse relationship between the influences of physical and social factors on food-web organization and function at river-road junctions (common nodes) within entire river networks. In high-elevation, high-energy (erosive) streams, we expect that social effects (*e.g.*, fish and shell-fish harvesting, introductions of non-native species) dominate changes in the species distributions because of easy access for people to intensively harvest river-based food and for frequent recreational uses near numerous small roads. In low-elevation, low-energy (depositional) streams, physical effects (*e.g.*, channel and hydrologic modification) dominate changes in the species distributions although land uses and other types of human impacts may become important in watersheds with high densities of roads. We will test a series of explicit hypotheses to compare and contrast the hydrology, geomorphology, visitor behavior, and food web structure at river segments and river-road junctions within these overlapping networks. These hypotheses have policy relevance in terms of the level of development that is allowed in currently unroaded watersheds.

The tropics provides a natural laboratory to study biocomplexity due to high biodiversity and rapidly increasing human density. Our case study site offers both of these features in a spatially compact set of adjacent, well-studied watersheds. We will conduct our field studies and calibrate our sub-models in three adjacent watersheds in northeastern Puerto Rico that have land uses that range from high-density urban to pristine tropical rain forests. The integrated model will then be tested in a fourth watershed that contains the same mix of land uses found in the adjacent watersheds. Northeastern Puerto Rico is a good natural laboratory due to rapid spreading of urbanization and sub-urbanization with an associated hierarchy of road networks that modifies the natural landscape and places people closer to natural resources. Being in

a coastal environment in proximity to rain forests, there is a steep land rent gradient that compresses the transitions from one land use to another. Similarly, the topographic steepness results in numerous, distinct transitions from one biological community to another in a short distance.

## CONCEPTUALIZATION AND THEORY

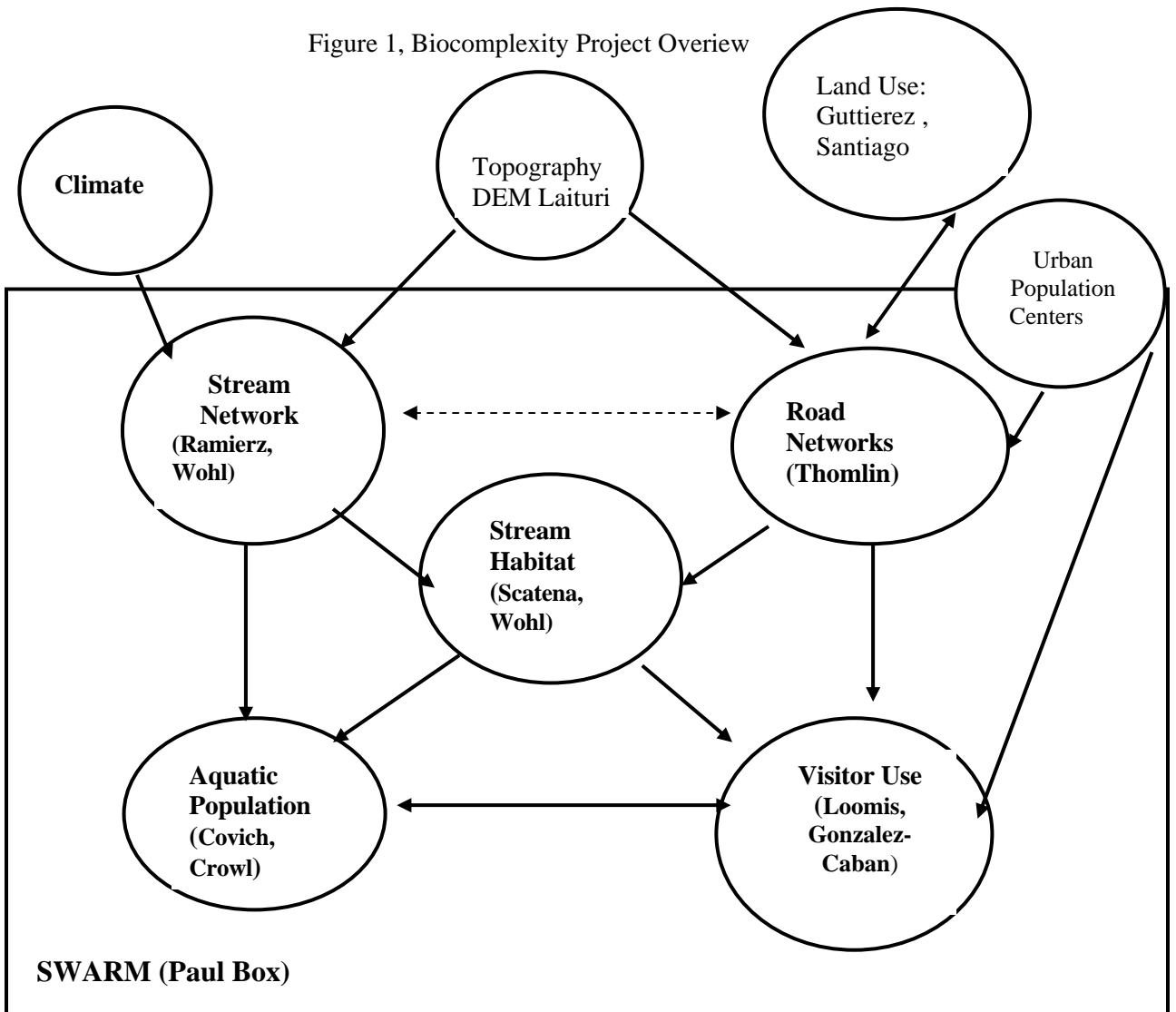
We will integrate physical, biological and social systems by incorporating the results of field studies into a unified individual-based model. In this framework agents interact by a set of rules or functions. These rules describe how each type of agent (physical, biotic and human) operates. These rules include not only the direct actions of the agents, but also interactions of the agents with each other. In the past, these individual-based models were applied separately to biotic and human systems [28]. Using an established individual-based modeling protocol called *Swarm*, [28, 123] (see website <http://geohive.nr.usu.edu/pr>) we will integrate the physical, biotic and human agents as interacting components of a single ecosystem. We will model operation of physical processes of river networks through energy minimization [177, 178, 179]. We will also model operation of biotic organisms within these rivers using time and energy as our common currency. Furthermore, we will model human agents' behavior through time and energy trade-offs in attainment of human objectives. A common linkage between biota and humans is the road network that provides humans access to river networks and influences land-use development.

**1. Research Integration and Project Management Plan.** Figure 1 below illustrates the interconnections between models and field studies by each PI, who will coordinate data collection and development of particular submodels. Ramirez, Wohl and a graduate student, will lead analysis of stream channel networks using Optimal Channel Network models (OCN) that combine climatic inputs (*e.g.*, rainfall), topography (Digital Elevation Models or DEMs) and concepts of optimal energy expenditure to derive channel and network geometry [177, 178, 179]. Tomlin and his graduate students will lead the development of road networks over time using raster based techniques and inputs of topography, land-use, and population centers developed from *Xplorah* by Gutierrez and Santiago at the Graduate School of Planning, University of Puerto Rico. Outputs from both the OCN models (*e.g.*, discharge, stream power, slope) and road densities from the Optimal Road Network (ORN) model will be combined by Scatena and Wohl using empirical field data and physical habitat models (PHABSIM) developed by the U.S. Geological Survey and recently modified by Scatena and Johnson [233], to model the quality of stream habitat for aquatic organisms (*e.g.*, shrimp) and recreation (*e.g.*, swimming). In this Stream Habitat model, habitat quality will be evaluated on the basis of physical features (*e.g.*, depth, volume, velocity, riparian conditions etc.) conducive to both recreation and aquatic organisms. Covich and Crowl and their graduate students will model use of stream habitats by aquatic species such as fishes and shrimps that are harvested by local fishermen. Recreational visitors to rivers who fish and swim in the rivers will be interviewed by Loomis and Gonzalez-Caban along with graduate student at UPR. They will develop and implement visitor surveys to estimate a Travel Cost Method recreation demand model utilizing the output from the Stream Habitat model (*e.g.*, stream depth, velocity), diversity and abundance of aquatic organisms, and Optimal Road Network (*e.g.*, travel times and costs) to parameterize the attraction of various points in the stream network for various types of recreational use (*e.g.*, swimming, fishing, etc.). The spatial and temporal distributions of the aquatic organisms will be derived from field data by Covich and Crowl, as well as data on road infrastructure from Laituri's GIS analysis. Likewise, output from Stream Habitat model combined with information on visitor use and the location of the pools within the Optimal Channel Network models will be used to compare the predicted and measured population structure of aquatic organisms at various locations within the landscape. Land-use changes at the parcel level will be modeled using the Von Thunen land-use transitions from population centers, as determined by road access and associated economic returns per acre [78, 227]. CO-PI's at UPR will use the *Xplorah* spatial decision support system that has been calibrated for Puerto Rico to link changes in social and economic processes associated with changes in the road network to land use changes. The *Xplorah* model uses economic forces such as dollar returns per acre, spatial interaction models, and cellular automata to model land use and their transitions.

All modeling efforts will initially be developed from field studies in four adjacent watersheds that range in land use from urban (high road density) to moderately developed (medium road density), to rela-

tively pristine tropical rain forest (low road density). The aquatic and human populations will be examined using individual-based models that work within the physical framework of pool habitats and are dependent on the configuration of the stream and road network. Rules for all sub-models will be implemented as integrated components of an individual-based model, where dynamic populations and dynamic landscape processes will run concurrently, using *Swarm* [176] and the Kenge libraries [27] to integrate agent-based models, cellular automata, and GIS in a common framework. After individual models are developed and integrated they will be tested by predicting outcomes in a fourth, relatively unroaded watershed, the Rio Fajardo. We will then use our integrated models to simulate future landscape development with various roading options.

Figure 1, Biocomplexity Project Overview



This project is well within the scope of the biocomplexity program in that it involves an interdisciplinary team that includes a hydrologist, two geomorphologists, two geographers, two economists, a science-education specialist, a water-quality specialist, two aquatic ecologists and a computer information specialist. The project provides graduate student training in all of these fields. We will focus on developing network models that will test present and future human impacts on tropical watersheds. Simulations of population-scale and landscape-scale dynamics will provide null-models to guide new field studies and experiments. Finally, through these model simulations, we will explore how various environmental policies may be used to manage current and future aquatic resource demands in tropical rainforest ecosystems.

**2. Organization and Measurement of Network Structures:** River and road networks vary in their complexity, which is a function of physical terrain complexity as well as economic forces and types of land uses. Structural and functional complexity are measured by several metrics: network circularity (reconnecting loops), centrality of nodes (numbers and locations of edge nodes relative to converging interior nodes), link lengths, rates of directional fluxes, maximal capacity of fluxes (floods or traffic congestion), resistance to flow along segments (debris dams or congestion), degree of node interconnectedness relative to possible connections (connectance), and alternative-distance measures between source locations and destinations. We define **common nodes** as locations where river and road segments are either in close proximity or directly intersect. These common river-road nodes constrict the width of larger river channels, floodplain habitats, and of tributary channels at river-road intersections (bridges and culverts).

**3. River Networks:** River networks are dynamic systems with complex branched structures that, in their undisturbed state, exhibit a high degree of regularity and spatial organization [98, 124, 125, 130, 177, 178, 179, 222, 223, 224, 242, 260, 261]. Their structure and channel hydraulics can be related to the hydrology and sedimentology of their watersheds by fundamental physical principles. The optimal, or equilibrium, structure of river networks can best be described as dynamic, with short-term adjustment due to variation in streamflow, sediment load, and human interference, present together with a long-term continuous evolution of the drainage system. In addition, other constraints (climate, geology, vegetation, human interference) can control river network adjustment. In any natural river system, fluctuations will occur about the characteristic average behavior in response to fluctuations in the controlling variables and the resistance and susceptibility of the river system to change [148, 177, 178, 179].-

**4. Road Networks:** Road building is expanding globally [35, 58, 126, 275], and is disrupting river ecosystems [142, 180, 268, 276], imposing greater and greater ecological and economic costs [139, 140, 173]. Roads represent structured networks relating to rates of flow and intensities of use. A hierarchy of road widths and permanence (paved versus unpaved) characterizes the intensities and frequencies of use as well as responses to barriers and congestion. In general, road networks develop an increased number of nodes as human population densities increase and as land cover shifts from natural vegetation to agricultural and residential. Although road grids are well studied in terms of traffic flows [12, 13, 17, 30, 38, 39, 85] rarely has any research integrated river networks and food webs. In mountainous areas the road network is largely controlled by the physical terrain (steepness of slopes, geology). In gentle sloping terrain, social inputs (*e.g.*, infrastructure demands) predominate in building and maintaining road networks. Energy expenditures for road construction will follow predictable relationships with physical terrain based on economic costs and benefits of alternative routes. Because small and large effects aggregate within road networks over time and space, entire ecosystems can be transformed by social processes that control and are controlled by road access [62, 103, 164, 170, 172, 177, 182]. Road networks change land uses and lead to floods, erosion, nutrient enrichment, and landslides [134, 187, 268]. Increased sedimentation adversely affects downstream channel morphology, biota, water quality, and water supply [84, 134, 180].

**5. Species Networks:** The various ways that species interact and form food-web assemblages have predictable, self-organizing structures. We use **species networks** to define this food web structure. Food webs are hierarchical assemblages of producers and consumers that are widely studied as a means of comparing how energy flow and nutrient cycling are related to the number of interacting species [20, 70, 113, 193, 194, 206]. Conceptually, food webs have been viewed either from the **bottom up**, with control from energy and nutrient inputs that regulate plant growth, or from the **top-down**, with control by

predators over herbivorous prey populations. The main features of food web resilience are the number and strengths of linkages among species. The types and numbers of linkages (connectance) within food webs change the pathways and rates of energy flow, especially when certain species or size classes are harvested. High trophic complexity is typical of stream food webs [55, 209, 210]. River-based food webs generally show clear compartmentalization, with predation from fish having large impacts on invertebrates at low elevations, while invertebrates dominate energy flow at middle and upper elevations (especially in channel segments above barriers to fish dispersal). Low-elevation, coastal rivers support a greater variety of fish species, many of which spend only a brief part of their life cycles in brackish or marine waters to feed on freshwater resources [52]. Energy subsidies (from externally produced, riparian leaf litter) are likely to be more important in smaller, high-elevation tributary streams than in larger, low-elevation rivers. Those food webs composed of native aquatic species are expected to affect natural capital such as habitat quality, food-web structure and function, recreational resource use (*e.g.*, habitat attractiveness).

**6. Road-River-Social Network Interactions:** Overlapping river and road networks physically direct flows of water, sediments, aquatic species, and people within the entire landscape. The drainage network provides the basis of a nested spatial hierarchy at landscape, stream reach, and pool scales. Nodes of both river channels and roads form hierarchically ordered structures that influence social and economic uses of watersheds (*e.g.*, in terms of visitor access to aquatic habitat and visitor harvesting of aquatic organisms). Roads can also divert runoff from streams and hillslopes to other nearby stream channels at lower elevations [134, 268] and change channel widths, pool depths, and size spectra of substrata. Debris dam formation (accumulation of woody debris and leaf litter deposited at high flows) at culverts can create other barriers to movement of fishes and other freshwater organisms among pools within the channel during low flows. Movements of sediments, nutrients, and aquatic species through river channels represent optimal-energy constraints (based on travel time and travel costs) to reach optimal destinations relative to starting locations and other individuals. These constraints are similar to how people move along roads subject to traffic jams and travel costs as they decide when and where to use river habitats [13, 38, 65, 72, 75, 269].

Rivers represent optimally structured networks related to volumes and rates of flow as determined by geology, vegetation and climate. In steep, wet terrain the main physical factors of channel properties are the seasonal flow regime [208] and landslides [142, 143, 144, 145, 146, 239]. Roads affect channels by directly and indirectly altering these factors. **Direct effects** occur when roads: 1) decrease local infiltration capacity and intercept subsurface flows, thus increasing surface runoff [267]; 2) increase sediment yield through erosion of an unpaved road surface [5, 24, 85, 167, 168]; 3) restrict or destroy the riparian corridor by occupying part of the valley bottom [273]; 4) create changes in channel cross-sectional geometry or downstream conveyance of water and sediment at road crossings [88, 229, 230]; and 5) induce changes in downstream hydraulic geometry and drainage network properties by altering flows, thereby effectively changing the spatial distribution of drainage density. **Indirect effects** occur when roads: 1) destabilize hillslopes and increase landslide magnitude and/or frequency [134, 142, 268]; 2) constrict channels, creating highly turbulent flows that form potential barriers to upstream and downstream movements of riverine species (disorienting migratory species responding to directional flows, *i.e.*, rheotaxis); 3) facilitate agricultural or urban development, which tends to increase sediment [95, 266] and water yield, respectively; 4) create recreational access at common nodes, especially consumptive recreation use; and 5) increase economic returns per acre and hence induce land use intensification. Thus, river-network distributions of energy and material flows as well as aquatic species and human activity can be hydrologically altered by road networks. Ultimately, as discussed below, interactions between river and road networks potentially affect aquatic food web structure and function.

**7. River-Road Interactions with Species Networks:** Despite the documented effects of road networks on streams, migratory salmonids, and a few other aquatic species [10, 83, 84, 104, 134, 164, 192, 240, 251, 271] we know little about the cascade of multiple effects of roads and people on river-based food webs. We anticipate that people modify natural patterns of food-web organization and persistence through harvest of species and alteration of water quality through increased sedimentation from erosion of river banks and riparian areas. The amount of recreational harvesting as well as species

introductions are almost certainly a function of accessibility derived from road access. The numbers of visitors to a specific common node will likely increase as road density increases and, over time, will alter habitat quality and species composition that, in turn, affect food-web structure and function. As numbers of visitors increase at common nodes, the likelihood of introductions of non-native species of fishes and invertebrates increases. These species can alter river ecosystems and recreational benefits [138, 150, 186, 221]. Native biotic community hierarchies in food webs will likely be further disrupted by recreational over-harvests of predatory fishes at river-road access points. Impacts of introductions and over-harvest at common nodes located downstream will generally have critical influences on upstream movements while impacts at common nodes located in headwaters will likely limit habitat availability, composition of species networks, and food-web structure [4, 14, 26, 242].

**8. Integration via *Swarm* Individual-Based Models.** Once the underlying physical, biotic and human relationships and their associated feedback mechanisms have been calibrated using our field data, they will be integrated via the *Swarm* modeling environment. Individual-based simulation is an essential tool for analyzing biocomplexity. This approach focuses on how system properties emerge from traits of individuals and their dynamic interactions. These models have provided insights to ecological systems [71, 123], economic systems [245] and the interplay of economics and biology [6]. Models and embedded-agent behavior can be subject to inferential hypothesis testing as well [6, 219]. *Swarm* is a software system that provides a virtual workbench for designing and implementing agent-based simulation models. *Swarm*'s key components include conventions modeling agents, their actions, and schedules by which they produce "swarms" of interactions within and between agents. Interaction between each member of the team and the *Swarm* programmer will translate the physical, biotic and human relationships with their associated feedbacks into a set of individual agent-based rules. The rules will reflect the objective of the agent (*e.g.*, maximize net energy), the interaction of individual agents within a given population (*e.g.*, shrimp) and between populations (*e.g.*, visitor effects on shrimp populations). This simulation program will then be run to observe the spatial and dynamic interactions associated with the interplay of the hydrology, biology and human uses. To address policy relevant choices before decision makers in Puerto Rico, we will use this model to predict changes in water and habitat quality, biotic communities, visitor use and land use change in the unroaded watershed that would result from roading.

In order to test our overarching hypothesis, we will compare the predictions of the full interaction model of all the agents to our field data versus predictions with one of the three main categories of agents removed (*e.g.*, road network, visitors, biotic communities). We expect there to be less divergence between predicted behavior of agents and field data with all agents and full complexity, than with one set of agents removed.

**9. Summary:** To understand present and future impacts on the natural capital of species networks we evaluate whether: 1) rivers and roads generally avoid obstacles and follow paths of least resistance (optimal energy expenditure); 2) when roads intersect river channels (with bridges, tunnels, and roadbeds) they alter river structure and function in ways that can be predicted from knowledge of the network structure; 3) access to rivers by humans is concentrated in areas where river and road networks have overlapping segments (common nodes); 4) intensities of human impacts (*e.g.*, recreation, harvesting aquatic species, introducing non-native species, increasing erosion and nutrients) are related to distances of these common nodes from population centers; and 5) aquatic species move both upstream and downstream within river networks to find optimal locations to complete their life cycle (*i.e.*, feed and reproduce). Many of the preliminary data necessary to quantify these relationships already exist. With this information, we will develop a series of interacting agent-based models that will allow us to depict current patterns of human uses and their consequences, as well as simulate possible future scenarios. Our modeling framework will also allow us to present visualization of probable effects on the aquatic environment as well as how various environmental policies may limit future impacts.

## METHODS AND MODELING

**1. Project Organization:** Our group synthesis provides an opportunity to coordinate our previously independent studies of hydrology, geomorphology, ecology, economics, and educational outreach. Our research will be integrated conceptually and quantitatively to ensure that our results will be greater than

the sum of our individual efforts. Measures of uncertainty will be incorporated through use of long-term data on climatic variables, water quality data (dissolved oxygen, turbidity, nutrient concentrations), aquatic species composition, and frequencies of road use with analysis of weekly, monthly, annual, and interannual variability. We will use theories of social and natural hierarchy, optimal network formation, and distance functions to integrate field-based hydrology, geomorphology and ecosystem measures with economic and statistical models [1, 15, 80, 115, 170, 193, 194, 196, 264].

**2. Study Site:** We selected four river networks in Puerto Rico that have similar elevational gradients, hydrological regimes, steep-headwater channels, drainage areas, vegetative cover, food-web composition, and seasonally defined recreational uses. They differ in road densities and access by visitors from roads. Land uses (urban, rural and natural tropical forest) in each of these four tropical coastal watersheds reflect elevation, with human developments primarily along the coastal plain. The area has a legacy of data-rich studies with decades of long-term research (> 60 years) on precipitation, flow regimes, [32, 165], watershed dynamics and land uses [162, 232]. Precipitation, ranging from mean annual 5 m of rainfall at higher elevations to 3 m at lower elevations, is seasonally and spatially variable and daily discharge is highly variable [90, 91]. Drainage networks range in elevation from cloud forests at 1000 m down to the ocean within 20 km. This range of elevation encompasses land-use transitions from urban population densities along the seacoast, estuaries, and large rivers to more dispersed human use of suburban, rural, and forested areas. Much of the study area, the Luquillo Experimental Forest (LEF), is part of NSF's Long-Term Ecological Research network [231, 233], a US Geological Survey research site, and UNESCO Man and the Biosphere Reserve. Puerto Rico's population density (400 people per km<sup>2</sup>, one of the highest in the world) provides a template for studying the relationships between people and geomorphic, hydrologic, economic, and ecological effects of roads on river networks. Centers of human population are concentrated near river outlets along the coast. River discharge is a major source of municipal water supply for San Juan and other communities (natural capital valued at \$24 million per year) and a significant source of recreational fishing and swimming. Previous surveys of the public's willingness to pay to maintain one of Luquillo's rivers for recreation estimated the non-market value at \$11 to 28 million for Río Mameyes [101, 157], indicating a high level of local interest in sustaining the river and ecosystem services. Visitors access the forest by use of 49 km of paved roads and numerous unpaved roads [192]. This complex road network accommodates more than 3.8 million residents and tourists [73, 162, 248]. Many people, including 14,000 tours by school groups, stop at the LEF's El Portal Interpretive Visitor Center to learn about rain-forest ecology and biodiversity.

This coastal montane site is a natural research and teaching laboratory. Our four study watersheds, Río Espíritu Santo, Río Mameyes, Río Icacos, and Río Fajardo, have road densities that vary from high to moderate to low, to very low, respectively. This range in road density lends itself to testing our hypotheses (listed below) without having to actually manipulate the forests or roads in the area. GIS data layers, long-term data on river discharge, water quality and biotic data on many of the species that comprise the aquatic food webs are available [52,53, 54, 215].

**3. Modeling River and Road Networks at Nested Scales:** Drainage networks naturally develop that are most efficient in delivering water and sediment loads to the catchment outlet [147, 177]. Efficiency refers to the work performed in transporting water and sediment, and the rate and distribution of energy expenditure. Concepts of energy expenditure are used to theoretically derive the downstream hydraulic geometry exponents observed in natural river networks [177, 178, 179]. Road networks are also expected to have similar traits that control their topology and how they affect rivers at common nodes. Optimal channel network (OCN) models will be used for quantitative analysis of the response of this complex system of interacting networks and as a virtual laboratory to explore hypotheses. Energy-based analysis will be used to compare roads with other natural and economic inputs in the forest [235].

Rodriguez-Iturbe et al. [224] postulated three optimality principles that define the optimal topological structure of a network and its channel characteristics, as well as deriving other important properties of drainage networks. Their work led to the definition and modeling of optimal channel networks (OCNs) that exhibit remarkable similarities with river networks extracted from digital elevation models (DEMs) in their fractal aggregation structure and other empirical geomorphological properties [224]. OCNs can be simulated by: 1) minimizing the total rate of energy expenditure; 2) using physically based models of water and

sediment transport in network and catchment development; or 3) using models of self-organized criticality with a stable landscape dependent on a critical erosion threshold. Molnar and Ramirez [178] recast the optimality principles into a local and a global hypothesis. The local hypothesis states that a river network adjusts its channel properties towards an optimal state in which the rate of energy dissipation per unit channel area is constant throughout the network. The global hypothesis states that a river network adjusts its topological structure towards a state in which the total rate of energy dissipation in the network is minimum.

The optimal, or equilibrium, structure of river networks can best be described as dynamic, with short-term adjustment due to variation in streamflow, sediment load, and human interference, present together with a long term continuous evolution of the drainage system. Thus, the local optimality hypothesis addresses the short term adjustment of channel geometry and roughness in response to short term fluctuations in discharge and sediment load. The global optimality hypothesis addresses the long term adjustment of the topological structure of the river network in response to geologic factors, continuous erosion, and long term changes in the runoff amount and sediment supply [178].

Our road-modeling effort will start by drawing inferences from the historical development of roads throughout the study area. This will enable us to identify the fundamental principles that are likely to underlie any near-future road-building activity in this area. By employing those principles under current and projected conditions, we expect to be able to reasonably predict the nature and location of future road networks. The road network model will be implemented using a raster-oriented GIS employing a cartographic modeling methodology [250]. It will encompass three major components including: (a) a set of travel destinations such as human settlements, ports, production sites or visitor attractions; (b) a set of geographic impedance factors indicating the incremental cost of travel throughout the study area in terms of measures such as time, money, and/or energy per unit of physical distance; and (c) a set of initial travel loads indicating the numbers of people, vehicles, or other items about to travel from designated locations. In its simplest form, the model will iteratively accumulate travel costs around selected destinations in a cost-minimizing manner and then use the resulting travel-cost surface to optimally route specified loads toward those destinations. This technique will be used in a variety of settings, ranging from attempts to explain historical road patterns to simulations of anticipated travel by recreational users with removal of existing roads in environmentally sensitive areas and addition of roads in currently unroaded areas. More sophisticated variations on the road network model will also be used to identify sub-optimal routes, to account for emergent effects (such as either increased impedance or channelization due to heavy flow volumes), and to examine changes in overall transport patterns.

Road and river interactions on each other and physical effects on aquatic habitat will be integratively modeled via a set of linked relationships in the *Swarm* model. We will define channel-response time to a landslide disturbance and the effects of greater road density on landsliding and on channel characteristics. At the reach or segment scale, the morphology of stream channels and adjacent floodplains affects the type and intensity of human and aquatic use. For example, flow depth and velocity alter aquatic habitats and locations suitable for swimming. We will model and quantify reach-scale interactions by choosing a series of channel reaches with roads and without roads. For each channel reach (50 m in length) at common nodes, we will measure downstream gradient, active-channel width, flow depth, abundance of large woody debris, pool volume and pool infill-sedimentation, bedform characteristics (type, wavelength, amplitude), substrate type, sinuosity, percent unstable bank, and ratio of active-channel width to valley-bottom width. Because there is likely to be high variability in channel characteristics, we will collect at least 10 replicates in each of the four major sampling categories (high-gradient with roads; high-gradient without roads; low-gradient with roads; low-gradient without roads). We will measure pool habitats and species composition at, above, and below all the major categories of road crossings. We will then test whether the channel features above and below the road crossing are different in each of the four major categories. CSU's civil engineers will work with Penn's geographer (Tomlin) to use GIS technologies to determine whether road crossings are randomly located with respect to channel morphology, or whether roads are consistently placed at specific channel features (*e.g.*, single or convergent river segments, waterfalls). The testing of these hypotheses will allow us to develop a model of physical hillslope-channel processes in the study area. This physical model provides the basis for our comprehensive model of landscape interactions.

**4. Food Web Dynamics, Aquatic Interactions and Human Disturbance:** To model elevation functional group distributions stepwise logistic regression analysis will be used. Presumed variables include stream size, pool depths, and waterfall heights. Predictive equations will be generated in a nested hierarchy within lower-, mid-, and upper-elevation sections and along entire drainage networks. We will develop food-web models for the lower, middle, and upper sections of the streams that characterize species abundances and interaction strengths using matrix projections. Upstream linkages will be modeled through stage-structured life history changes in relative abundances while downstream linkages will be modeled through larval drift. Human disturbances will be incorporated by comparing residual errors for sites with measured human impacts (harvest and nutrient inputs) from the predicted distributions and interaction strengths based on the original modeling efforts. To determine how physical variables associated with minimally affected sites control and predict aquatic food-web structure and function, we will collect information of species presence/absence as well as biomass estimates for the dominant species. In addition to standing stock estimates, we will use mark-recapture techniques to determine the amount and rate of turnover within the aquatic food web. Data on channel substrata, gradient, stream width, depth, and discharge will also be collected at each site. We will use multivariate analyses to create a suite of composite response variables (*e.g.*, number of species, relative abundance, biomass) to measure patterns and responses of stream communities within the drainage network.

To differentiate and quantify patterns of relationships between human visitation, nutrient concentrations, and food-web composition among sites with various levels of road access logistic regressions and discriminant functions analysis will be used. Similar analyses will be used to evaluate elevation gradients for the same suite of variables. Multiple regression analyses and analysis of covariance will be used to quantify functional relationships needed for other modeling approaches. Multivariate analysis will be used to reduce the dimensionality of response variables among classes of variables (food-web composition).

We will conduct a series of experiments to determine the effects of different levels of human disturbance on biotic responses. We will vary physical disturbance (swimming and wading) to determine impacts on three sizes of natural stream pools (at river-river connections and away from roads). Three levels of human disturbance (derived from the social sub-model database of observations) will be used as three treatment levels. One day prior to treatment, all decapods and fish in these pools will be marked (elastomer dye) and released. Following the treatment, decapods and fish will be re-sampled in the experimental pools and those pools upstream and downstream from the treatment to determine rates of any directional movement in response to disturbance. These data are necessary to determine how movement dynamics can influence rates of detrital processing and grazing and overall food-web structure. We will use a split-plot ANOVA with repeated measures to test for density and duration impacts on emigration rates and distances moved. The results of these analyses will be input into *Swarm* to allow interaction and feedback effects to be simulated with changes in roads and human uses.

**5. Social Dynamics and Human Interactions at Network Scales:** At landscape scale, we will focus on how road facilitated access enabling land use changes and recreation visitation affect aquatic species populations and the feedback of changes in abundance of aquatic organisms affects future recreation use. Previous economic estimates for recreational demand [87, 154, 155, 156], have not determined how feedback loops from different types and locations of recreational use and land use changes alters food webs and influences future recreation use. We will use visitor counts and survey responses of visitors at recreation areas throughout all four watersheds that vary in the degree of road access as a key element of our analysis of ecological and social relationships. Based on these data, we will use individual based recreation travel cost demand models [132, 151, 200] to estimate how natural landscape features (*e.g.*, waterfalls), biotic productivity, facilities (*e.g.*, picnic sites) influence how people distribute themselves spatially and temporally along road networks for different activities. These surveys will extend the design of previous successful (73% response rate) surveys of one of the four study rivers [136, 157] to provide data for model variables such as recreational activities, duration of stay, species harvest, trip costs, and benefits to the visitors in the form of their willingness to pay. Target visitor sample sizes will be 200 on each of the four rivers for a total of 800. The per-river sample size proved adequate in the Loomis and González-Cabán analysis of one of the four study rivers. In-person interviews proved successful at

eliciting complete information from respondents and allowing for clarification of any ambiguities in the survey. Information on visitors' recreational activities and duration of visits will be obtained to model future distributions with simulated changes in the river and road networks. Last summer we established protocols for determining distributions of visitors and initiated interviews with anglers [136].

We will use logistic and multiple regressions to test which variables best explain and predict visitor use. The GIS modeling will provide spatially explicit data on road network and recreation facilities data for use in the visitor demand model. The influence of roads, facilities, species harvest, and natural features will be statistically modeled, and the output of this model will be used as an input into the species diversity statistical models. Native and non-native species richness would be modeled as a function of the estimated visitor use and GIS-based spatial data on road network, natural features, elevation, turbidity, and instream flows. Both sets of interacting relationships (*e.g.*, direct effects on harvest and indirect habitat effects on biotic species, and biotic species on visitor demand) will be input into *Swarm* so as to simulate dynamic feedback cycling over time. Within *Swarm* we can also simulate the ecological effects of closing road access on visitor use and biotic communities via changes in foodwebs. This analysis completes the feedback loop, whereby policies controlling visitor access, visitor use levels, and distribution can be a tool in maintaining ecosystem functions and services.

The role of roads in spurring land use changes from agricultural, to residential, to commercial in the lowlands and coastal plain will be evaluated using GIS and the economic geography concepts of VonThuenen [111]. Introduction of new roads changes the land rent gradient, and can lead to land use intensification [189]. CO-PI's at UPR will use the *Xplorah* spatial decision support system that has been calibrated for Puerto Rico to link changes in social and economic processes associated with changes in the road network. *Xplorah* uses mathematical and rule based models to describe and predict how social and economic processes change the physical environment at different spatial scales. The model has four modules that link economics, demographics, transportation and land use together with each other and GIS data on physical suitability of lands for different land uses. The driver of land use change in the model is economic returns per acre, which is influenced by the road network, demographics and land type (*e.g.* coastal versus mountainous). *Xplorah* will allow us to predict dynamic land use changes since it incorporates the influence of current proximate land uses on future land uses as well as resulting feedbacks. The GIS map visualization capabilities of *Xplorah* will allow us to display alternative road building policies on land uses. Land use change will then be modeled as a component in *Swarm* building upon the previous individual agent based models [227].

**6. Coupling of Landscape, Aquatic, and Human Interactions:** GIS and *Swarm* will provide complementary and linked analytical models for integrating field data within the river and road network structure. [37, 77, 103, 109, 151]. GIS-based modeling is well developed for network analysis and for determining variance among statistical distributions of landscape elements [218, 255, 256]. This project will use novel applications of GIS for analysis of tropical river networks in an integrated physical and social perspective. Spatially referenced data on slope, aspect, soil types, riparian vegetation, river locations, and proximity to roads are available through the USFS and other sources (USGS, EPA). High-resolution digital elevation models (DEM) will be used to infer stream drainage patterns, which we will compare to existing mapped rivers and streams, based on the USGS digital line graphs [74]. We will ground truth streams inferred from topography (but not currently mapped) to determine their status as perennial or ephemeral. The resultant drainage network map will be overlain on a road map (based on digital line graphs) to identify connections of the two networks. This river-road map in turn will be overlain on the topography, and paired sample sites will be selected. Each pair will comprise upstream and downstream samples associated with a river-road connection and a river-river connection at similar elevation. These paired sites will be used to compare ecological functions at the two different kinds of connections. Upstream and downstream flow in the stream network, and two-way flow in the road network, will be modeled using simple impedance functions for each segment in the network [30, 122]. This modeling will allow us to incorporate the effects of waterfalls, water diversion structures, debris dams in the streams, and other blockages to traffic flow (landslides, road works, or peak travel-time bottlenecks). The flow networks of the intersecting systems will be overlain to identify points at which the impacts of one network upon the other will be maximized. The results from the *Swarm* simulations

can be output as spatial data layers for integration into the GIS model. This will allow the possibility of visual display of the dynamic interactions of the aquatic and human uses.

## RESEARCH HYPOTHESES

In using individual agent based models and GIS networks to evaluate our hypotheses, we will measure and model the spatially explicit physical and social relationships among aquatic species and visitors at accessible aquatic habitats. We will compare dynamics at undisturbed river-river nodes with river-road nodes associated with varied intensities of human impacts from major, paved roads and minor, unpaved roads. As the frequency and density of these common nodes increases with grid-based networks, we expect that social factors become more important than physical factors in determining patterns of energy flows. We also expect that social factors often function in a direction opposite to physical factors when both networks are dendritic. Network theory suggests that sensitivity to variable flow is greatest at sites of centrality and convergence (nodes) within a drainage network where multiple, larger tributaries converge. We anticipate that the sediment introduced to steep channel reaches (links) by landslides will significantly decrease habitat diversity and persistence, alter species interactions, and increase barriers to species migrating upstream and downstream. High-elevation, steep-gradient streams with immobile bedrock and boulder channels may be less likely to be modified by roads. Social factors will play a role in roadway locations and influences on the species network. We have four hypotheses to integrate our research on how physical and social variables interact within overlapping river and road networks to control the number of species in aquatic food webs:

### **H1. Roads have different direct physical impacts (e.g., run-off and bank erosion) at low and high elevations in coastal montane ecosystems.**

**Rationale and Approach:** This hypothesis is focused on understanding the landscape level interrelationships of river-road networks. River networks in coastal-montane regions such as Puerto Rico are comprised of steep, narrow channels at upper elevations and low-gradient, wide channels in lower elevations. The high-gradient segments constitute transport reaches [182] and are less sensitive to increases in water and sediment yield. The hydraulic energy expenditures and land use in steep, wet terrain result in roads that are likely to affect the high-elevation channel reaches by increasing landslide disturbance, or by roads crossing the channel and impeding the movement of water, sediment, and organisms (*e.g.*, culvert effects). Steep channel reaches with adjacent roads will have significantly less pool volume and more waterfall-type-barriers. To test this hypothesis we will model channel energy expenditure at the landscape scale and conduct field surveys of stream segments with and without road connections to determine if these high-energy sites are resistant to human-induced physical impacts.

Low-gradient, low-elevation channels generally have high water and sediment yield, which are likely to cause channel change. These low-gradient reaches also have more mobile substrates, and a greater likelihood of being braided, than analogous steep-channel reaches without roads. Low-gradient, low-elevation reaches with road crossings will have significantly less pool volume and more channel instability than analogous channel reaches without roads. Along coastal segments, greater degrees of human influence will likely correspond to significantly more channel erosion and less stable channels. Low-gradient reaches will be impacted by both increased water yields associated with high road densities (in some areas by reticulate road networks associated with urbanization) and increased sediment yields from upstream. At low elevations, where human population centers are often located, roadbeds are generally oriented parallel to river channels. These roadbeds can laterally constrict floodplains thereby decreasing important connections between rivers and floodplain wetlands. Further habitat fragmentation can result from road, bridge, and culvert construction that restrict connections among migratory pathways.

### **H2: The amount of human social activities at any location within the drainage network depends on the structure of the road and river networks; however, the type of human activities differs from the high-elevation headwaters to the low-elevation reaches.**

**Rationale and Approach:** This hypothesis is focused on understanding how the topography and character of river and road networks influences human visitation, and how these visitations affect species

networks. The amount of human visitation to any river segment will be a function of natural channel features, instream flow, precipitation, harvestable species, facilities, roads, and distance to urban population centers. Modeling road traffic and recreational visitation will allow us to test different scenarios that alter road access and change road network structure for different seasons and periods of time by closing gates or simulating landslides and floods. Road densities and traffic are usually higher at low to mid elevations than at high elevations. Thus, we anticipate that the types and frequencies of road-based social activities will have disproportional effects on food webs in tributary streams at these mid and low elevations. Over time, high frequencies of visitation will likely result in more introductions of non-native species in low- and mid-elevation streams. Persistent non-native species together with increased nutrient and sediment loading from river-bank erosion, and removal of top-level native species or predators from food webs will likely cause food-web dysfunction and breakdown of aquatic ecosystem services (biotic productivity, re-oxygenation, and decomposition). Non-native species may increase "ecosystem fragility" because of the lack of evolutionary adaptations for sustained functionality in response to natural and human disturbances over time. The control of nutrient cycling and other ecosystem functions within the river network are likely to change in site-specific ways because of these anthropogenic impacts. These changes may result in complex threshold effects and time lags in how biotic communities function. Our modeling will include multiple physical, biotic, and social variables and multi-year time frames for analysis. Impacts of human use will be scaled by the size of the drainage area above the site due to expected hydrologic control of physical disturbance.

**H3: In headwater streams, social factors (e.g. number of visitors, amount of harvest) are more important in affecting food webs than physical modifications to channels that are more important in the lower-elevation river reaches.**

**Rationale and Approach:** Coupling of human and natural dynamics is spatially context dependent. Locations within the river network, nutrient concentrations, and turbidity influence aquatic species behavior (feeding, reproduction, predator avoidance) and biological productivity. This productivity, in turn, will likely influence visitation frequencies that, over time, will alter the harvestable species and other ecosystem services (decomposition of organic matter, re-oxygenation of pools). Under large, highly variable discharges, aquatic communities in river ecosystems tend toward self-organization because physical scouring results in species assemblages dependent on dispersal and colonization dynamics [183, 216, 244, 249]. Dispersal upstream and downstream from nodes will be predicted based on geomorphic variables and our energy expenditure models. The presence of partial (e.g., small waterfalls and debris dams) or complete barriers (e.g., large waterfalls and landslide-debris flows) as well as complexity of substrata, frequency of flooding, and intensity of scour of channel segments, will all influence the long-term dispersal and persistence of native and non-native species. These characteristics are likely most important at intermediate elevations. Some human impacts (fishing, erosion, nutrient inputs) may be more intense along rivers at lower elevations while others (swimming and picnics) may be more frequent at upper elevations. Scenic attributes (waterfalls at higher elevations, viewing overlooks) may attract certain visitors. Although increased road densities provide greater recreation access and may result in higher levels of recreation use, the recreation quality and benefits per visitor may not be higher in less accessible areas due to trade-offs between values of greater water clarity, species abundance and less crowding. Using *Swarm* to simulate a population of individual visitors with a variety of preferences (values of group affinity vs. solitude, ability and willingness to walk to isolated areas, tolerance for noise or encounters with other recreators) models can predict distributions of people and road use [28,67,68,98,99,100,112,].

**H4. Integrated physical-biological-human model will yield more accurate predictions and reduced variance of habitat quality, biotic and human use predictions than will individual disciplinary models.** This overarching hypothesis will be tested by comparing predictions of road development induced changes in habitat quality, biotic communities and visitor use in our undeveloped study site watershed to actual impacts in our developed study site watershed. The experimental design relies upon existing natural variation in the level of development in our case study site. Within this natural variation are different levels of road density and road type within a network structure that reflects a hierarchy of land uses and

geomorphic and riverine features. We will test the accuracy of predictions and variance of predicted values of key variables from the *Swarm* model using all categories (physical, biotic, human) of interacting agents versus predictions with one class of agents removed. We expect more accurate predictions and less variance even though the full model will be more complex, because what otherwise would be missing feedback effects in the individual disciplinary models (e.g. visitor use as an explanatory variable in biotic systems) would be included in the full model.

## EDUCATIONAL OUTREACH PLAN

The concept of interactive physical, biological, and social networks provides an opportunity for students to solve problems regarding human impacts on natural ecosystems and enhances the teacher's ability to develop fundamental concepts in natural and social sciences. We will develop a multi-university, graduate seminar and a capstone senior seminar for undergraduates. We will also develop bilingual learning modules for a wide range of high-school students and teachers. Our past experience shows that a question-based approach encourages students to learn both important concepts and inquiry skills, as recommended by the National Science Education Standards (NRC, 1996). This approach relies upon making connections with students' prior knowledge and experience [19, 31]. We will incorporate students and teachers from four rural high schools near our study sites and will add teachers and students from Colorado high schools. Both students and teachers will participate in annual workshops to contribute towards the development of modules on GIS and network analysis. Several members of our group have had considerable experience in developing new learning modules that use spatial information technologies to integrate concepts, applications and diverse sources of data in ways now recognized as productive [106, 110, 236, 256]. We have brought together compatible interests and abilities to create new ways to link modules so as to emphasize quantitative methods in an interdisciplinary framework. Workshops will be coordinated by CoPIs with the Center for Science, Mathematics and Technology Education (CSMATE) at Colorado State University. [See letters in Supplemental Documents.].

Students and teachers will use GIS technology and computer simulations to investigate the consequences of individual decisions. We will provide downloadable copy of the simulation software that teachers can install with a user interface where they can change parameters such as road location, numbers of visitors, kinds of activities, etc. They will then be able to answer questions such as: "What are the effects on land uses, visitation and water quality if a new road is built or an existing road closed?" "What are the effects of removing predators or grazers on nutrient cycling and water quality within a network of streams and rivers?" and "Do changes in water quality feed back to alter the food web at different positions within overlapping river and road networks?" Drainage networks will be compared with changes in flow regimes that are linked to road locations, human access, and multiple inputs of nutrients from several sources. Our simulations will provide student-centered learning in a context of ecosystems, economics, and consumer behaviors. These modules will be tested and modified in our web-based multi-university seminars and will be linked to more intensive reading and writing assignments based on discussion of several interdisciplinary studies of complexity theory [8, 11, 32, 75, 95, 116, 117].

## WORK PLANS AND TASK ORGANIZATION

### Year 1

**1) Field Studies:** Stream habitat surveys from undisturbed headwaters to urbanized coastal plain in the three baseline drainages will be initiated by Scatena and graduate students and coordinated with the stream network analysis of Ramirez and Wohl. Covich and Crowl will survey aquatic organisms in same drainages and compile information on spatial and temporal distributions of species as well as feeding relationships (based on more than 10 years of data).

**2) Model development and integration design:** Ramirez and Wohl will initiate their modeling within the undisturbed portions of the Río Mameyes and Rio Espíritu Santo drainages where sufficient data are available to define natural reference conditions. Tomlin will analyze historic maps and initiate modeling of road network development while Box will design the *Swarm* framework for integrating physical, aquatic, recreation and land use models. Gutierrez at Puerto Rico will provide spatial data layers that characterize the existing land use in and around our study area. We will further develop our methods

for visualization and analysis of our physical terrain models to identify and quantify spatial attributes (e.g., steep slopes, river access points from nearby roads) that may influence species distributions within the river network.

**3) Education:** Co-PIs will develop the seminars for the multi-year, Multi-University Biocomplexity Training Program at CSU, UPenn, UPR and USU. The first year's seminar will focus on the theoretical basis of biocomplexity and involve graduate and undergraduate students in assembling baseline databases to develop functional relationships within the biotic sector that can be used as initial rules within *Swarm*. This educational outreach will be coordinated with CSU's on-going Research Experiences for Undergraduates (REU) in Water Research directed by Ramirez. The initial Education Modules and Workshops will be developed and coordinated by Covich, Laituri, Loomis, and Box. We will begin to build learning modules and incorporate research and teaching questions into a GIS-based format accessible to non-specialists.

#### **Year 2:**

**1) Field Studies:** Loomis and González-Cabán will initiate visitor counts, pretest visitor surveys and pretest interview procedures with people fishing and visiting the rivers with two Puerto Rican graduate students. Stream habitat and aquatic population analysis will continue with the additional emphasis on working in known recreation areas so the visitor counts and biotic population data can be temporally and spatially linked in developing functional relationships in individual agent based model.

**2) Modeling:** River network and road network models will be linked with stream habitat models to evaluate how habitat quality (e.g., depth, velocity, volume etc.) varies with the attributes of river and road networks (e.g., density, slope, fluxes of people and water etc.). Crowl will coordinate the development of the river productivity submodels in collaboration with Covich and Scatena. Gutierrez will use *Xplorah* to provide a description of future lands uses in and around our study area. Tomlin will use this information in his roads model to characterize how future road networks may develop in response to anticipated land use changes. Linkages between the sub models as well as GIS analyses and development of refined *Swarm* model individual resource rules will continue as a group effort. We will analyze seasonal and event-driven discharge relationships using visualization and simulation techniques to identify thresholds in river flow variations that alter spatial relationships within the river and road networks.

**3) Education:** Multi-University Biocomplexity Seminar series will continue and focus on how Biocomplexity can be measured and quantified. While Luquillo will be the case study, we will invite speakers from other Biocomplexity programs to present other case studies. At the end of field season, a workshop/meeting with local resource managers and teachers will be convened in Puerto Rico to communicate results and obtain ideas from teachers on what results and format would be useful to present on project website for teaching purposes.

#### **Year 3:**

**1) Field Studies:** Loomis and González-Cabán, with student research assistants, will conduct visitor interviews at all four watershed sites. Scatena, Covich, and Crowl will conduct field studies of the Fajardo watershed. Experiments at sampled recreation areas with marked individual fish and decapods will be set up in pools of different sizes to determine how human disturbance influences feeding behavior as well as upstream and downstream movement. Video-recording of behavior will be incorporated into learning modules and the university seminars to illustrate how recreational uses and non-native species alter food web composition and function. The visitor sampling and fish mark-recapture studies will be coordinated in time and location so they can be linked as functional relationships in the individual agent based model.

**2) Model Integration:** After visitor survey, and mark-recapture experiments, the results of visitor regression models will be used for evaluating ecological effects of visitor distributions on species composition and ecological functions. The two visitation and species diversity regression models will be used to simulate the consequences of selective road closures on visitation and then species diversity in those watersheds. The results from tasks 1-2 in Year 3 will be formalized into *Swarm* functional relationships that include feedbacks between water quality, biotic resources, visitor use, and their mutual interactions upon each other. Specifically, rules governing river and road networks, habitat usage by aquatic organisms, visitor use of roads and rivers regression and land uses will be integrated into *Swarm* and simulations run to characterize the dynamic interactions and feedback effects.

**3) Education:** The Multi-University Biocomplexity Seminar series will focus on testing initial modeling predictions and presentations of graduate students research. Teachers and students will be invited to participate in education workshops to further develop and test the applications of computer-based learning modules and network simulations.

**Year 4:**

**1) Field Database:** The completed data will be organized for publication of electronic data sets. Additional data will be collected to test model predictions in Fajardo watersheds.

**2) Integrated Modeling and Hypothesis Testing:** The integrated *Swarm* model will be calibrated and tested in the Fajardo watershed. The final *Swarm* model will be used to test the five research hypotheses. *Swarm* simulations will be used to predict environmental effects of roading currently unroaded watersheds and closing existing roads to provide information to policy makers in Puerto Rico such as the U.S. Forest Service that manages the uplands and the Commonwealth of Puerto Rico that controls land use zoning in the lowlands. *Swarm* and GIS models suitable for classroom use and answering “what if” questions will be developed.

**3) Education:** The Multi-University Biocomplexity Seminar will involve presentation of research results at an organized session at a professional meeting such as the Ecological Society. Manuscripts will be prepared and submitted to peer-review journals as well as a report on the professional meeting session results as a review paper suitable for teachers and policy makers. A final workshop with teachers demonstrating the educational products and a separate workshop with Puerto Rico policy makers to disseminate the results will be conducted.

**VII. RESULTS FROM PRIOR NSF SUPPORT AND RELATION TO PROPOSED RESEARCH**  
**Long-Term Ecological Research (LTER) Grant to the University of Puerto Rico and the International Institute of Tropical Forestry: DEB-9411973 and DEB-9705814; \$200,000 to Covich, Crowl, and Scatena (1994-2001).**

Investigators from more than 12 academic institutions were supported by the Luquillo LTER Program. Covich, Crowl, and Scatena, PIs on this biocomplexity proposal, have worked together since 1988 and have received support from the Luquillo LTER project. Eight graduate students and 10 undergraduates (three from the University of Puerto Rico) assisted us. Most of the LTER research focused on biotic responses to disturbances from Hurricane Hugo (in 1989) and Hurricane Georges (in 1998). Recent publications (>20 since 1994) are listed [3, 34, 36, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 59, 60, 61, 62, 63, 197, 198, 228, 229, 230, 231, 232, 233, 234, 235, 263] (authors in bold) in the References Cited (section D, p. 16). We examined how geomorphic changes in stream channels along with pulsed inputs of sediment, woody debris, and leaf litter to headwater streams altered species abundance within invertebrate and fish communities. Based on a survey of 22 streams in four watersheds we selected four streams that represented the range of variation of biotic communities for long-term study. We sampled 28 pools bimonthly along an elevation gradient from 260 m to 550 m to determine community responses to disturbances [53, 54]. We documented food web dynamics [52, 61, 211], seasonality of reproduction [132] and effects of wood and leaf-litter inputs before and after storms [217]. Longitudinal patterns of species diversity demonstrate that food web structure becomes less complex at higher elevations, especially above steep waterfalls and other geologic features that control upstream migrations of fishes, decapods, and gastropods. We measured species-specific differences among species in detrital-based food webs. Our previous research provides data that will be useful in the proposed study of a larger network-based set of sites and lower-elevation food webs.

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