

# The Emergence and Evolution of Ecosystem Functioning

A Proposal Submitted to the Andrew W. Mellon Foundation

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Date

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## **1. Introduction**

For decades, the disciplines of population biology and ecosystems science have developed with inadequate contact between them, seemingly addressing distinct problems on different scales. That situation has changed dramatically in the past decade, even as ecosystems science has become more global in scope, and as much of population biology has relied increasingly on molecular techniques. Indeed, the need to deal with phenomena across these distinct levels of organization and complexity has made more obvious, and more urgent, the importance of finding ways to scale, from the small scale to the large, and from the individual to the biosphere.

The time is ripe for innovative, integrative approaches to such integration from theoretical as well as empirical perspectives. Princeton certainly is not alone in its attention to these problems, but has unique capabilities to develop novel approaches in understanding and conceptualizing the dynamics of diverse systems. Our group has over the past year and a half developed strong partnerships reaching from autecology and population biology to hydrology and biogeochemical cycling, and involving both theoretical and empirical approaches. We propose to use this foundation to further develop a collaborative training and research program at the interface between population biology and biogeochemical cycling, with central focus on training graduate students and postdoctoral fellows. In this way, we expect to develop a cadre of young scientists well-grounded in both disciplines, and with the interdisciplinary perspectives that are necessary for future intellectual leadership in ecology and biogeochemistry.

The general themes of this project will involve an understanding of community and ecosystem structure and functioning, across systems and across scales. We shall particularly be interested in

grasslands, temperate and tropical forests, and marine coastal and off-shore systems. In all of this research, the work will be soundly based in empirical work, but also closely linked to the development of theoretical and quantitative models. In particular, we will build on techniques we have long been developing for modeling spatially distributed populations, and for scaling from microscopic to macroscopic phenomena. Many of these techniques, and many of the empirical patterns that we will address, have been developed under prior Mellon funding. Specific projects follow.

## **2. Savanna-grassland borders**

The ecotone from tropical forest to savanna and grassland is perhaps the least understood biome boundary. As one progresses from the forest edge into the savanna and grassland, rainfall decreases only slightly, but ecosystem function and biodiversity change dramatically. For example, the amount of carbon in living biomass falls from forest to grassland by approximately an order of magnitude.

There are currently three dominant hypotheses for this geographically sudden shift in ecosystem structure and function, each focusing on the factors that maintain the transitional savanna. The niche-partitioning hypothesis holds that grasses are better competitors for shallow water, while trees are better competitors for deep water and light. The successional hypothesis states that grasses are early successional specialists whereas trees are late successional specialists. The fire hypothesis posits two positive feedback loops involving fire (1) grasses are dominant competitors with frequent fire and dominance by grasses increases fire frequency, and (2) trees dominate with infrequent fire and reduce fire frequency. Outside of the transitional savanna, the local dynamics are the same under each of the three hypotheses: competitive exclusion of dominant grasses in the forested region to competitive exclusion of trees in the grassland. This shift is caused by increasing importance of shallow water in the niche partitioning hypothesis, decreasing speed of succession relative to disturbance in the successional hypothesis, and increasing frequency of the dry conditions favoring fire in the fire hypothesis.

From a mathematical perspective, the three hypotheses are almost as different as it is possible to be. If the local dynamics of the savanna were modeled by two differential equations, with one equation for grass abundance and the other for tree abundance, then the savanna would correspond to a stable internal equilibrium under the niche partitioning hypothesis, a single stable boundary equilibrium under the successional hypothesis (with random perturbations by disturbance to maintain the grasses), and a pair of simultaneously stable boundary equilibria under the fire hypothesis. These represent each of the qualitatively different patterns that can be exhibited by simple competition models such as the Lotka-Volterra equations.

When placed in a spatial context, the three hypotheses should also imply qualitatively different patch dynamics and function at the ecosystem level. Under the niche hypothesis, patches of forest or grassland in a savanna region reflect underlying edaphic variation in water availability and so should remain spatially static. Under the successional hypothesis, patches of grassland and forest should fluctuate constantly in a shifting successional mosaic. Under the fire hypothesis, patches should tend to remain dominated by whichever type colonizes first, but grow very slowly.

These expectations are complicated by the possibility that the vegetation of the forest-grassland transition directly affects the climate. Recent studies at Princeton combining atmospheric, hydrological and ecological modeling raise the possibility of important feedbacks at three different scales. Over scales of tens to hundreds of kilometers, forest vegetation promotes increased regional rainfall. This raises the possibility of positive feedback similar to that in the fire hypothesis, but involving precipitation as well as fire, and operating at much larger scales. Over scales of one to tens of kilometers, forest-grassland patchiness appears to reduce meteorological thresholds for convective storms and increases local rainfall. At fine scales, micrometeorological conditions are considerably dryer near the edge of a forest patch than in the center, and grassland fires affect forest edges even if they do not propagate within forest patches. We have not yet begun to elucidate the possible interactions among these factors and mechanisms of the niche partitioning, successional and fire hypotheses.

We propose to develop and study a suite of models of the tropical forest-grassland ecotone. These will range from simple models of single mechanisms or combinations of two, to fully spatial models that combine vegetation, fire and patch dynamics with meteorology and hydrology at a variety of scales. The purpose of the work will be to characterize the range of possibilities, given currently available data, and then to identify the set of field measurements that will best discriminate among the alternative explanations. We will also collaborate with a variety of groups who are working on the problem empirically. These include investigators with the NASA LBA project in northern South America (Pacala is an LBA investigator), R. Holdo who is a Princeton graduate student working in Zimbabwe, and the South African group currently funded by the Mellon Foundation.

### **3. Terrestrial nutrient cycles**

Our understanding of terrestrial nutrient cycles is undergoing dramatic change. It is becoming increasingly clear that there exist dramatic, predictable, yet largely unresolved, variations in nutrient cycles across terrestrial ecosystems globally. For example, our own studies in South America and Hawaii (funded by the A.W. Mellon Foundation) have shown that temperate and tropical forests display dramatically different patterns of nutrient loss and plant-microbe-soil nutrient relations. It is also increasingly clear that many of these global-scale variations in nutrient cycles are seriously at odds with predictions from our most modern ecosystem models. Together, these observations suggest that our traditional models are inadequate for explaining global patterns in nutrient cycles within terrestrial ecosystems.

We propose to address these questions by adopting a combined empirical and theoretical approach. We seek to better characterize similarities, differences, and limits to variations in nutrient cycles and element ratios within and among different terrestrial ecosystems, with particular emphasis on forests. We also want to make use of measures of isotopic ratios of single nutrients and elements to understand how terrestrial ecosystems differ in sources (e.g., the isotope oxygen 18 can discriminate between atmospheric and soil sources of nitrate) and transformations (e.g., denitrification, nitrogen fixation, etc.) of key nutrients. Such combined

analyses of abundances of major nutrients (carbon, nitrogen and phosphorus) and stable isotopic ratios (nitrogen and oxygen) have been *essential* for shaping the modern view of how the global ocean functions as an integrated biogeochemical ecosystem. An analogous approach has not yet been attempted for explaining globally broad variations in the function of terrestrial ecosystems; we here seek to initiate such an approach.

In addition to the empirical characterization of broad geographic patterns in nutrient cycles and isotopic ratios, we will develop a series of models that explore how ecosystem-level patterns develop and are maintained based on local organism-nutrient interactions and top-down feedback effects. By linking to population biology and physiological ecology, we seek to replace standard “black box” approaches to modeling ecosystem nutrient cycles with new conceptions based on individual organism-nutrient interactions, capable of explaining the emergence of global patterns in nutrient cycles and isotopic ratios. We are especially interested in whether and how different physiological strategies among terrestrial plants and microbial communities act to either magnify or eliminate particular ecosystem-scale properties (e.g., nutrient limitation or element ratios), and how these interactions depend on Darwinian selection at the level of individuals. But we are also equally interested in the alternative condition, in which macroscopic ecosystem properties emerge as a consequence of internal scaling rules, with little or no link to Darwinian selection.

Patterns of nutrient cycling and isotopic ratios integrate processes that occur across a range of spatial and temporal scales. Globally, nitrogen isotopic ratios found under different environmental boundary conditions depend intimately on the internal ecosystem structure and function. For instance, oxygen isotopes of nitrate can be used to determine the degree to which ecosystem-scale losses of nitrate are linked to atmospheric nitrate inputs vs. internal nitrogen recycling. In addition, comparisons of nitrogen isotopes between ecosystem inputs and outputs reflect the balance and internal cycling of nitrogen. These ecosystem-scale patterns are, in turn, linked to individual organism-nutrient interactions in local environments. For example, isotope measures of plant tissues can address questions such as "How does the relative importance of nitrate as a plant nutrient change as a function of environmental variables?" At the scale of microbes, isotopes can be used to indicate the nature of N cycle processes in soils, reflecting both variations in sources and kinetic conditions. Finally, at the biochemical scale, stable isotopes

provide a novel tool for the functional comparison of enzymes and the physiological function of different organisms.

The multiple spatial and temporal scales that affect both nutrient distributions and isotopic ratios have often been interpreted as evidence for the limited applicability of such analyses for understanding contributions from specific mechanisms. Yet, this limitation has not been a serious obstruction in the efforts to understand nutrient cycles in the global ocean system. Rather, geographically broad analyses of nutrients and isotopes have revealed strong and predictable trends across different environments that, in turn, have led to important insights for understanding the underlying processes. In truth, we do not know whether terrestrial systems will similarly display clear and predictable patterns of co-variation between nutrient and isotopic information. Yet, since nutrient cycles and isotopic ratios represent the integration of a large number of interactions within ecosystems, it is reasonable to expect that broad and predictable patterns will naturally emerge in response to macroscopic variations in ecosystem function.

We propose to undertake a broad cooperative study of the constraints of nutrient cycles and isotopic ratios of nitrogen and oxygen. The breadth of the proposed project has both philosophical and practical motivations. From a philosophical perspective, the most meaningful view of nutrient cycles are holistic. It is clear that fundamental biochemical aspects of N cycle transformations influence the greater spatio-temporal scales, including ecosystems and the global biosphere. Moreover, it seems quite likely that these influences are reflexive, with aspects of the global biosphere influencing the competition, interaction, and evolution of the fundamental biochemical processes. The practical perspective is related: regardless of the initial goals of a study, because of the mutual relevance of the different scales of the N cycle, the best studies are those that are free to evolve in any direction (a degree of freedom that does not typically accompany an NSF-funded study).

#### **4. Cross-scale comparisons of community structure**

Complementing the work in the previous sections, we will also extend work carried out with Mellon support to elucidate the influence of exogenous and endogenous patchiness on ecological communities, with a focus on temperate and tropical forests, and the intertidal. Under Mellon and other support, we have built a variety of theoretical models (see for example Keymer et al. 2000; Chave et al. 2001) to explore how communities are organized in space and time. These models have allowed us to explore the role of tradeoffs, such as between fecundity and competitive ability, and the importance of disturbance and natural enemies. We have constructed a suite of models, from stochastic point processes to those involving fixed grids, as well as continuum approximations. These models in particular have been used to develop characteristic species distribution patterns (Chave et al. 2002), scaling laws (Chave and Levin to appear), and evolutionary templates (Levin and Muller-Landau 2000a, b).

Early models of this type were developed for the intertidal (Levin and Paine 1974) and for forests (Botkin et al. 1972, Pacala and Silander 1985, Pacala 1986; see also Deutschman et al. 1999), and a great deal of progress has been made in relating to data both in the intertidal and for terrestrial systems. We would now like to extend this work in three ways. First of all, building on Hedin's tropical forest work, and the models for nutrient dynamics that we have begun to develop, we propose to modify these approaches for tropical forests, with characteristically different disturbance regions, and in which natural enemies play a unique role. Secondly, we want to build on the generic approaches to explore the role of heterogeneity in underlying conditions, separating the influences of intrinsic and extrinsic factors as a function of the scale of investigation. Thirdly, building on work carried out with Ran Nathan, Roni Avissar and others for trees (Nathan et al. in press), and analogous work now under development for the near-shore marine environment, we propose to couple Lagrangian models of transport of propagules with models of community development to provide integrated views of systems dynamics at macroscopic scales.

## 5. Bibliography

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Andrew W. Mellon Foundation Proposal  
Simon Levin, Principal Investigator

The Emergence and Evolution of Ecosystem Functioning

Three Year Budget

	Year 01 09/01/03	Year 02 09/01/04	Year 03 09/01/05	3 Year Total
<b><u>SALARIES</u></b>				
<b>Postdoctoral Associates</b> (2 Associates per year)	68,400	72,200	81,200	221,800
<b>Computer Technician</b>	<u>2,500</u>	<u>2,500</u>	<u>2,500</u>	<u>7,500</u>
Total Salaries	70,900	74,700	83,700	229,300
Fringe Benefits	<u>23,680</u>	<u>25,025</u>	<u>28,374</u>	<u>77,079</u>
<b>Total Salaries and Fringe</b>	<b>94,580</b>	<b>99,725</b>	<b>112,074</b>	<b>306,379</b>
<b><u>STIPENDS AND TUITION</u></b>				
<b>Graduate Students</b>				
Stipends (3 students per year)	70,500	75,900	78,300	224,700
Tuition (3 students per year)	<u>85,800</u>	<u>88,200</u>	<u>90,600</u>	<u>264,600</u>
<b>Total Stipends/Tuition</b>	<b>156,300</b>	<b>164,100</b>	<b>168,900</b>	<b>489,300</b>
<b><u>RESEARCH AND TRAVEL ALLOWANCES</u></b>				
Postdoctoral Associates	8,000	8,000	8,000	24,000
Graduate Students	12,000	12,000	12,000	36,000
Undergraduate Students	2,000	2,000	2,000	6,000
Travel for Program Director and Co-Directors	<u>4,000</u>	<u>4,000</u>	<u>4,000</u>	<u>12,000</u>
<b>Total Research and Travel Allowances</b>	<b><u>26,000</u></b>	<b><u>26,000</u></b>	<b><u>26,000</u></b>	<b><u>78,000</u></b>
<b>TOTAL COSTS OF 3 YEAR PROGRAM</b>	<b><u>276,880</u></b>	<b><u>289,825</u></b>	<b><u>306,974</u></b>	<b><u>873,679</u></b>
<b>COST SHARING BY PRINCETON UNIVERSITY (from central and departmental funds)</b>				
6/8 tuition per graduate student per year 3 graduate students per year	<b>64,350</b>	<b>66,150</b>	<b>67,950</b>	<b>198,450</b>
<b>REMAINING PROGRAM COSTS</b>	<b><u>212,530</u></b>	<b><u>223,675</u></b>	<b><u>239,024</u></b>	<b><u>675,229</u></b>

**NOTES**

Year 01 Full Tuition = \$28,600 per student  
Year 02 Full Tuition = \$29,400 per student  
Year 03 Full Tuition = \$30,200 per student

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Simon Levin, Principal Investigator  
Moffett Professor of Biology

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Michelle Christy, Director  
Office of Research and Project Administration

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Simon Levin, Principal Investigator

**Budget Notes**

**Salaries**

**Postdoctoral Associates:** The Program will support two Postdoctoral Associates each year. Salaries are based on an estimated increase in National Institutes of Health postdoctoral training grant salaries

Year 01        \$34,200 per Associate

Year 02        \$36,100 per Associate

Year 03        \$40,600 per Associate

**Computer Technician:** A computer technician will provide technical support to the Program's Postdoctoral Associates and graduate students.

**Fringe Benefits:** The fringe benefit rates established by the University are:

Year 01 33.4%        Year 02 33.5%        Year 03 33.9%

**Graduate Students:**

**STIPENDS:** The Program will provide full 12-months support for three graduate students per year. Princeton University provides stipend and tuition support for all science students during their first year of study. In their second year of study (Year 01 of the grant), students in the Program will be supported at the Pre-Generals stipend level. Following successful completion of the General Examination (which is normally taken at the end of the 2<sup>nd</sup> year of study), students will be supported at the Post-Generals level (Years 02 and 03 of the grant). The stipend scale as established by the University is:

Year 01    \$23,500    12 months    (\$17,700 Academic Yr; \$5,800 summer)

Year 02    \$25,300    12 months    (\$19,300 Academic Yr; \$6,000 summer)

Year 03    \$26,100    12 months    (\$19,900 Academic Yr; \$6,200 summer)

**TUITION:** The Program will provide 2/8ths of the annual tuition per graduate student. The remaining 6/8ths tuition will be provided by Princeton University from central and departmental funds.

Year 01        Full Tuition per student    \$28,600        2/8<sup>th</sup> tuition    \$7,150

Year 02        Full Tuition per student    \$29,400        2/8<sup>th</sup> tuition    \$7,350

Year 03        Full Tuition per student    \$30,200        2/8<sup>th</sup> tuition    \$7,550

**Research and Travel Allowances**

**Postdoctoral Associates and Graduate Students:** The Program will provide a research and travel allowance to postdoctoral associates and graduate students estimated at \$4,000 per person per year. This allowance will be used for research costs such as laboratory and/or field supplies and materials, computer equipment, services and specialized software, and domestic and international travel to research field sites and conferences.

**Undergraduate Students:** The Program will provide a small number of awards (for research materials and travel) to undergraduate students who are carrying out Program-related undergraduate theses projects under the supervision of Program faculty.

**Travel for Principal Investigators:** Up to \$4,000 per year will be available for travel by the Principal Investigators. These funds will be used to visit research field sites where the Program's postdoctoral associates and graduate students are carrying out projects. Project sites include U.S. locations (such as Hawaii) and international locations (such as Brazil and Chile).

**Cost-Sharing by Princeton University:** 6/8ths graduate student tuition will be provided by Princeton University from central and departmental funds.

Year 01	\$64,350
Year 02	\$66,150
Year 03	\$67,950