Title:LTER: LTER5: Understanding Ecosystem Change in Northeastern Puerto Rico
Institution: University of Puerto Rico-Rio Piedras
NSF Program:LONG TERM ECOLOGICAL RESEARCH
Principal Investigator: Zimmerman, Jess K.

Rating: Very Good

Review:

In the context of the five review elements, please
evaluate the strengths and weaknesses of the proposal with respect to intellectual merit.

Comments Overall

The LUQ LTER project has focused on how disturbances interact with land use to control the dynamics of an island wet tropical forests and associated tropical streams. One of the core historical strengths of this project has been the integration of the role that disturbances play in both forests and streams. These have been tied together with a series of long-term observations (forest dynamics plot, monitored watersheds), experiments (canopy trimming to simulate hurricanes), and gradient studies (forest elevation gradient). Forest dynamics have been modeled with a forest demography model and a trophic dynamics model. In this next three year period, two new experiments will be added: (1) a stream drought experiment in which streamflow is reduced by manipulation, and a forest throughfall reduction experiment in which rainfall is reduced by manipulation.

In this formulation (LUQ V) the project focuses on a compelling set of general questions that are of very high importance for tropical forest. Those are: (1) how changing disturbance regimes will affect forest biota and biogeochemistry, (2) how these disturbance regimes will interact with changing climate, and (3) how disturbances are influenced by either land use history or disturbance history. In this place-based study, the disturbances identified as most important are hurricanes and drought (both projected to increase). Effects of hurricanes have been the subject of previous LUQ work, while examination of drought is new. Examination of both is well justified and important. How disturbance regimes will change and how these will interact with climate in the future are major questions for this forest and for tropical forests in general. These questions are clearly stated and identified at the start of the proposal. The progression of the LUQ LTER is clearly explained.

The long term forest plots are valuable and need to be long term because disturbance ins infrequent. They provide an important insight into multi-year forest dynamics. The canopy trimming experiment is very creative and novel. The elevation gradient provides an important landscape perspective.

The new experiments proposed here will simulate droughts in small streams and in forest plots. They are somewhat modest in their ambition (a single 150 m reach of stream and a series of 3 x 3 m understory rain shelters). They are a good fit with the new emphasis on understanding drought and greater climate variability.

The site is unique and valuable in the LTER network in that it is a tropical forest site within the US.

Overall the scientific productivity has been strong, particulary work by Covitch, Crowell, McDowell, Silver, Uriarte, Walker, Willig and Zimmerman. Work was nicely synthesized in a recent (2012) book.

While the framing of this proposal clearly follows from previous work, in some ways it does not break a lot of new ground. But it potentially could by following up more explicitly on ideas raised in the introduction. There are three main points related to this.

1. The introduction postulates that novel ecosystems will develop from the separate and combined effects of increased drought and hurricane frequency. But what these novel ecosystems are is never clearly explained, even in the section on p. 23 when this is dealt with in detail. What are these new combinations of disturbances? Of forest tree species? Of stream assemblages under new and not previous existing flow regimes? How will these novel ecosystems differ from previous ones? How does their novelty affect their function? What, if any, generalities can be learned by observing these novel ecosystems develop in the context of an LTER where you have potential for experimentation and long term study?

2. The idea is raised that tropical ecosystems might be more sensitive to climate shifts than ecosystems in more temperate zones because tropical organisms face little intra-annual temperature variability. This is also not followed up on. For one thing, temperature change is not identified as a key element of study here. But does this idea also apply to droughtsùthat organisms are more sensitive if they see little intra-annual moisture variation? It's an interesting idea that could lead to more general understanding of ecosystems in general, but nothing in the project will explicitly test it.

3. The LUQ tropical forest reflects a particular circumstance (on an island, in hurricane belt). While this is a place-based project, little attempt is made here to explain how and if understanding of processes such as moisture variation in LUQ will lead to new insights about tropical forests in general. For example, drought in lowland tropical forests is moderated by deep rooting. Does this exist in PR? It's not stated. Strong work in stream demonstrated the importance of underlying geology on stream chemistry. How relevant is that to other tropical locations? In other words, some attempt to explain how understanding disturbance dynamics, response to drought and other factors known in detail in LUQ will lead to greater understanding of tropical forests in general is needed but mostly missing.

There are two additional ways this overall project framing could be strengthened.

1. Development of conceptual models for different subsections. For example, the idea that drought will reduce tree production on ridges (more drought stress) but increase production in valleys (less waterlogging stress) could be incorporated into a conceptual model that combines changes to soil biogeochemistry to make these predictions. Such as, on ridges, dry soils will get drier and methane and nitrous oxide fluxes will not change much, in valleys they will decrease because of increased soil oxygen status. This would be a more synthetic way of combining these interesting ideas.

2. The hypotheses do not make enough clear predictions that can be tested. It's not compelling to state that "droughts will alter the spatial dynamics of seedling survival and growth along catenas. (p. 11).

How can this hypothesis be truly tested if it is not more specific. Too many hypotheses are like this (e.g., 1a, 1b, 3a, 4, 5, 8).

Comments on Proposed Research

Proposed research on how drought will affect moist tropical forest is timely and important. The hypotheses that drought will result in decreased seedling tree growth and survival on ridges and greater growth and survival in currently wet valleys (by alleviating waterlogging) adds an interesting spatial component to this question.

For seedlings, this idea will be tested with an experiment that plants seedlings along an elevation gradient and then exposes them to experimentally reduced rainfall under rainout shelters. For mature trees, presumably (though it is not stated particularly clearly on p. 13), a somewhat parallel approach along the elevation gradient using forest monitoring plots will also examine mortality of adult trees. These two experiments are then tied together with SORTIE modeling to determine the future makeup of forest in this spatial and elevational context.

The small size of the rain reduction shelters limits work to seedlings instead of whole trees, which would be much more challenging but also much more interesting.

While this work is appropriate within the site-specific context of this LTER, two concepts that are mentioned but not particularly well explored here would increase the contribution of this work to our general understanding of forests.

1. Janzen's (1967) and Mora et al.'s (2013) ideas that moist tropical ecosystems are more vulnerable to climate shifts compared with temperate or arctic ecosystems because the tropics see little intra-annual climate variation are mentioned but not fully explored. This is a very big and important idea and zeroing in on how this work can test this idea would strengthen this project. This could involve, for example, creative comparisons with responses to variability in other forests of the LTER network or other sites. As written, this important idea is introduced, but not really tested.

2. There has been much excellent work on tropical forest responses to drought in other locations. An excellent one is Nepstad et al.'s (2007, Ecology 88:2259) work showing that deep roots buffer forest response to reduced rain and that drought takes multiple years to increase tree mortality. Deep rooting is an absolutely critical mechanism that controls drought response in lowland forests. It's important to place these Puerto Rican forests in perspective of other tropical forests. Does deep rooting occur? If not, how does that make them different from other large areas of global tropical forest. This perspective is needed to build a more general and predictive understanding, but largely absent hereùso this project's contribution to understanding tropical forest response in general is therefore reduced.

Drought influences a large number of biogeochemical processes affected by soil redox potential. This overall organizational framework is very sensible and strong.

However, here the hypotheses state that there are short-term and long-term responses to drought. In

the short term, soils are drier and more aerobic. This (like seedling and tree responses) has a spatial component. In the long term, lower NPP will decrease C inputs.

This section would benefit from two things: (1) a clear conceptual model (could be divided up into short- and long-term responses); and (2) a clear connection to how both the short- and long-term responses will be measured. As it is, a lot of measurements are proposed that aren't all clearly justified as testing some clear predictions.

Hypotheses 3a (ii) and (iii), and Hypothesis 3b are valuable and will test general ideas about how drought affects small streams. This would also benefit from some more holistic conceptual framing that links changes to production and leaf litter storage to food web structure.

The canopy trimming experiments are a unique opportunity to measure the effects of hurricanes on plant species dynamics, soils and fauna. This is integrated with soil modeling using DayCent model. This is also a unique opportunity to link post-disturbance changes to stream chemistry through process measurements that can infer effects at watersheds scales. It's a little unclear how that linkage will be made. The canopy trimming experiment does not appear to contain lysimetry or soil solution measurements that would explicitly make this linkage.

It's not clear what the microbial sequencing (p. 15) is testing or what soil enzyme measurements will reveal (p. 20).

One of the most interesting and generally applicable ideas in this proposal is the concept that responses to disturbance depend upon the previous disturbance and land use. New combinations of legacies will occur with climate change (and its control of rain and hurricanes). No specific statements are made about what these new combinations are likely to be and no experiments are proposed to test hypothesized responses. Rather, a series of modeling tests are proposed. It's stated that these will guide future tests of predictions against field data. It would be valuable to have some concrete examples of what kinds of tests those might be. As it is, this very exciting idea is raised but not linked to any clear way to break new ground on this issue in the context of this LTER.

Related Research

One of the great benefits of an LTER is the platform it provides for investigators to test a wide range of ideas within experiments or along carefully laid out gradients. This LTER is successful in that regard. It would be interesting to include some accounting of the number of investigators that connect to the LTER sites and bring new research support that contribute new measurements and new publications.

In the context of the five review elements, please
evaluate the strengths and weaknesses of the proposal with respect to broader impacts.

This proposal has a strong set of broader impacts. These include a schoolyard LTER program in which schools establish forest monitoring plots, the development of a midel school curriculum, an internship program for Puerto Rican students, research for undergraduate students and graduate student

research. These are described briefly on one page (p. 25). The use in a separate proposal to study how the LTER middle school curriculum influenced learning is a strength.

The location of this site provides a continuing excellent opportunity to connect with Hispanic students who are underrepresented in ecology and natural sciences. This project has an excellent record engaging a high proportion of underrepresented minorities.

Please evaluate the strengths and
weaknesses of the proposal with respect to any additional solicitation-specific review criteria, if applicable

This proposal contains components that are specific to LTER. It contains questions that can be addressed effectively only by long-term research. It contains descriptions of long term experiments and plans for their management over multiple years. The proposal contains measurements in core LTER areas but does not specifically contain any cross-site research.

Summary Statement

This is a strong proposal that asks important questions about how disturbance and climate influence tropical forest of Puerto Rico. It contains a strong science team and the study of disturbance is well integrated across forest and streams. It contains a very novel experiment on forest canopy trimming to simulate hurricanes and separate effects of canopy openness from deposition of material to the forest floor. New experiments will focus on effects of drought, both with a stream flow reduction and forest rain reduction.

Proposal weaknesses include the absence of well constructed linkages between more general ideas about how tropical forest ecosystems or forest ecosystems in general respond to disturbance and interactions with climate. Two potential larger conceptual frameworks are proposed, one that these interactions create novel ecosystems with novel vegetation dynamics and biogeochemistry, and another that climate shifts in tropical ecosystems should be more disruptive than to temperate ecosystems because of tropical forest organisms' limited exposure to intra-annual temperature change. Neither idea is developed in ways that explain how it can be tested with experiments or long-term observations. Although this focuses on drought effects, proposal also deals only in a superficial manner with how drought affects other tropical forests and how what is learned in Puerto Rico is or is not applicable elsewhere. The statement of hypotheses is often simply that things will change, which limits their ability to be clearly tested. Many sections of the research plan would benefit from more integrative conceptual models.