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Why Snails? How Gastropods Improve Our Understanding of Ecological Disturbance

Christopher Bloch

The concept of equilibrium—the idea that a perturbed system will tend to return to its original state—is the basis for many foundational theories in ecology. Yet, the spatial and temporal dynamics of ecosystems are strongly influenced by disturbance. In the ecological literature, a disturbance is most commonly defined as an event, distinct from ordinary demographic processes, that

alters population size, environmental conditions or resource availability. That is a broad definition, potentially encompassing everything from geologic upheaval or extreme climatic events to something as simple and localized as an animal digging a burrow.

Disturbances can prevent equilibrium, or, if extreme enough, even establish a new equilibrium. As such, they have potentially far-ranging effects on ecosystems. As human populations continue to grow, our ability to manage resources and preserve biodiversity

depends on our understanding of how disturbance affects natural systems. It is within this context that we study the effects of disturbance on terrestrial gastropods.

Gastropods (snails and slugs, the latter of which are really just snails that have lost their shells over evolutionary time) are excellent organisms with which to study the effects of disturbance. They are abundant and diverse and play important roles in ecosystem function by serving as prey for many other species and promoting the decomposition

of dead plant matter and the subsequent recycling of nutrients. What makes them ideal for studies of disturbance, however, is their dependence on environmental conditions. When a gastropod moves from one place to another, it does so by secreting a layer of mucus and using wavelike muscular contractions of its foot to glide across it. Consequently, movement is costly for gastropods in terms of water, and they are very sensitive to changes in the availability of water in the environment. If a particular disturbance greatly alters local climatic conditions, gastropods should be among the first organisms to show a measurable response.

In 1980, the National Science Foundation established the Long-term Ecological Research (LTER) Network, a series of research sites dedicated to studying long-term ecological phenomena. Today, the LTER Network comprises 26 sites in diverse ecosystems, including temperate forests, grasslands, deserts, barrier islands, coastal waters, arctic tundra and even urban communities. One of these is located in the Luquillo Mountains of northeastern Puerto Rico. Its location is fortuitous for several reasons. El Yunque National Forest, the montane rain forest where most Luquillo LTER research occurs, experiences a warm

Common Snails of El Yunque (Photographs by Jason Lech)



Polydontes lima



Nenia tridens

and wet climate throughout the year. As a result, gastropods are particularly conspicuous. Several species are large (with shells up to 60 millimeters in diameter), abundant and arboreal, making them easy to identify, capture and study. In addition, this site is subject to periodic hurricanes, landslides, droughts and floods, and it also has a history of human activity, including logging and agriculture. This makes it

to severe natural disturbances. In other words, the time necessary to recover from the disturbance is considerably less than the time it takes before a second disturbance occurs at the same location. For example, a major hurricane (Category 3 or higher on the Saffir-Simpson scale) strikes the Luquillo Mountains on average every 20 to 60 years, but the forest canopy recovers within five to 10 years.

composition different from those areas that did not experience extensive anthropogenic disturbance. Moreover, the most common tree species found in areas that were extensively altered by humans tend to be more susceptible to damage by hurricanes than are those that dominate areas with no anthropogenic disturbance history. Ultimately, this suggests that increasing human activity worldwide will have long-lasting effects that influence how ecosystems respond to natural disturbances in unexpected ways.

If a particular disturbance greatly alters local climatic conditions, gastropods should be among the first organisms to show a measurable response.

an ideal “natural laboratory” in which to study effects of disturbance on tropical forest ecosystems.

Initially, the Luquillo LTER project focused on understanding how tropical forest ecosystems respond to natural disturbances such as hurricanes, landslides, droughts and floods. It quickly became clear that ecosystems in the Luquillo Mountains are highly resilient

The story became more complex, however, as researchers investigated the interplay between natural disturbances and the history of human activity. The effects of human alteration of habitats (for example, conversion of forest to agriculture) have much longer-lasting effects than those of natural disturbances. Areas abandoned by humans in the 1930s continue to exhibit tree species

An important application of research at Luquillo LTER is to predict the consequences of environmental changes to ecosystem health and important services the forest provides to humans. For example, although El Yunque National Forest is the largest nature reserve in Puerto Rico, the surrounding region is experiencing rapid urbanization. Puerto Rico is one of the most densely populated places on Earth, with more than 400 individuals per square kilometer. Density is greatest in and around the capital of San Juan, a mere 48 kilometers from El Yunque, and growth is particularly rapid there. Consequently, the amount of water extracted from mountain streams in recent decades has increased considerably, even as average annual rainfall has slightly decreased.



Caracolus marginella



Alcaldia striata



Polydortes acutangula



El Verde Field Station, El Yunque National Forest, Puerto Rico (Photograph by Jason Lech).

Moreover, average temperatures have increased in the urbanized regions around the forest and may be changing in the forest itself. A clear understanding of the effects of these events is critical to our ability to forecast future changes in species diversity, ecosystem structure and, ultimately, the ability of the forest to provide ecosystem services to the growing human population of eastern Puerto Rico.

I began working in Puerto Rico in March of 1998, as a first-year Ph.D. student. Initially, I was not particularly

excited about the project, as snails are not the most charismatic of organisms. My perspective changed just six months later, when Hurricane Georges made landfall in Puerto Rico as a Category 3 storm, providing me with an unusual opportunity. I was lucky enough to inherit data from the same study plots stretching back to 1991. Because Hurricane Hugo (a Category 4 storm) had struck eastern Puerto Rico in September of 1989, I could examine long-term dynamics of gastropod abundance and diversity in the aftermath of two major hurricanes.

It is rare to have data that allow for meaningful comparisons between large, intense disturbances. Such disturbances are infrequent and difficult to study, so researchers often try to extrapolate and draw general conclusions from a single event. This is problematic, though, because different disturbance events, even of the same type, differ in their physical characteristics and historical context. For example, Hurricane Hugo was a more intense storm than was Hurricane Georges, but the forest it encountered in the Luquillo Mountains was also very different. Before Hugo, it had been more than 50 years since a major hurricane had struck Puerto Rico, so the forest in 1989 was tall and mature. The resulting tree damage was catastrophic: near the current location of my study plots, Hugo killed approximately 25% of trees and completely defoliated over 50%. In contrast, only ten years passed between Hurricanes Hugo and Georges, so the forest in 1998 contained a greater proportion of young, healthy trees and sustained much less damage. Trying to characterize the effects of hurricanes based on either storm alone would have ignored the fact that no two hurricanes are alike.

To date, I have focused primarily on three separate but related variables:



Pleurodonte caracolla



Oleacina glabra



Alcadia striata

abundance (both of individual species and of gastropods as a whole), diversity and spatial structure. Each of these addresses a slightly different aspect of responses to disturbance. Trends in abundance can reveal how resilient gastropod populations are to changing environmental conditions and enable one to predict which species might be most susceptible to novel disturbances. Changes in diversity at multiple spatial scales illustrate how the broader gastropod assemblage is affected. This may help to predict whether future disturbance events are likely to cause local extinctions. Examining the spatial structure of gastropod populations ties my other results together by allowing me to develop meaningful hypotheses about mechanisms that lead to local changes in abundance or diversity and about functional links between local populations.

In terms of abundance, different species of gastropods responded to hurricane disturbance in different ways. Some initially declined in abundance and slowly recovered over five to 10 years. Others were more abundant two to three years after disturbance and then declined back to their pre-hurricane population sizes. Still others displayed no obvious pattern at all, or a different pattern after each hurricane. The reason for this diversity of responses is that hurricanes primarily affect gastropods indirectly by modifying the environment. The storm itself kills or displaces relatively few individuals—primarily those unlucky enough to be crushed by debris or washed downstream. However, a hurricane has long-lasting effects on forest structure. It generates large openings in the forest canopy and deposits a great deal of debris on the ground. Over time, this process

affects gastropods in multiple ways. Conditions in canopy gaps are hotter and drier—and, therefore, more stressful for gastropods—than under intact canopy, yet the debris deposits provide food and shelter. As a result, gastropod species that are best able to tolerate desiccation are able to be most active and take advantage of the increased resources.

Despite the variety of responses exhibited by individual species, overall gastropod abundance displayed a clear and consistent trend. Abundance declined initially and then recovered over time. Remarkably, this recovery occurred at the same rate after each hurricane, despite the considerable differences between the two storms. In fact, even though I observed considerable seasonal and inter-annual variability, I was able to explain approximately forty percent of the variation in gastropod abundance from 1991 to 2004 based solely on how much time had elapsed since a hurricane. In more recent years, the trend of increasing abundance has disappeared, so dynamics are now dominated by seasonal variation and short-term responses to climatic conditions. For example, a particularly wet year will promote juvenile survival and lead to an increase in population size, whereas an unusually dry period will have the

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Subulina octona



Polydortes acutangula

opposite effect. In general, this suggests that gastropods will need no more than ten years for population recovery from even a severe hurricane.

The diversity of an ecological community can be characterized in two ways: species richness, which simply indicates the number of different species that are present; and species evenness, which

The number of species observed on the long-term study plots I sample has varied between eight and 16 since 1991, but I found no correlation with time since disturbance. In contrast, species evenness was greatest immediately after hurricanes, when gastropod abundances are low, but decreased over time thereafter as communities became

after a hurricane and the forest canopy recovers, environmental conditions improve and make movement through the forest easier for gastropods, allowing common species to become more widespread. This probably contributes to the ability of these common species to increase in abundance, as they are able to colonize areas of the forest that had been inhospitable. Most interesting to me, the rate of change in spatial structure of gastropod communities was the same after both hurricanes and did not differ among three regions that differed in their history of human activity. The latter result suggests that tree species composition, which still reflects the impact of humans over 70 years later, is less important in determining abundance and spatial distribution of gastropods than are local climatic conditions. Altered tree composition in forests where invasive species become established or where humans conduct modest silviculture, may have relatively little effect on gastropod populations.

Ultimately, all of this suggests that gastropod species native to the Luquillo Mountains are well adapted to hurricane disturbance and that extinctions are unlikely under the current disturbance regime. This optimistic conclusion is tempered, however, by the strong possibility that the disturbance

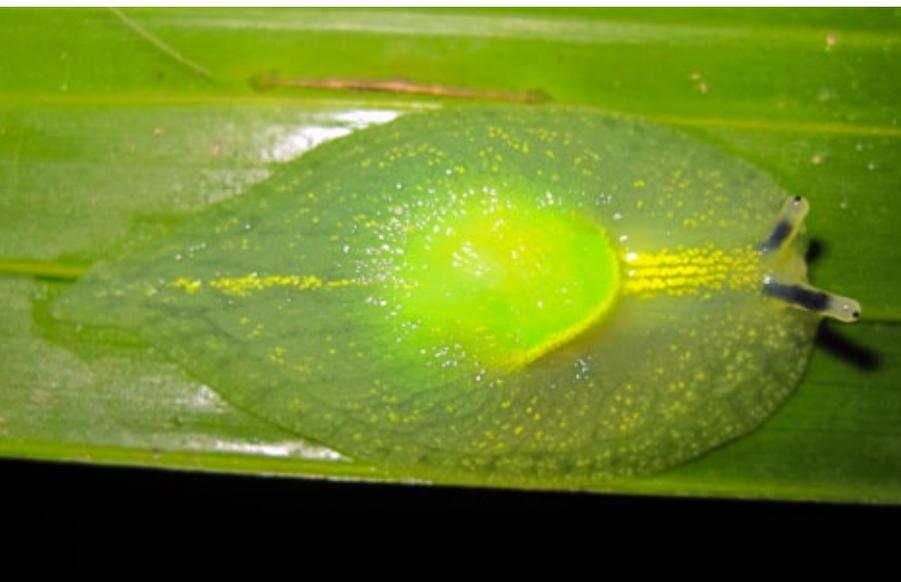
It is rare to have data that allow for meaningful comparisons between large, intense disturbances.

reflects the degree to which a community is dominated by one or a few species. For example, consider two communities: both support five species, but in one, a single species contributes most of the individuals, whereas in the other, abundances are nearly equal. Although species richness is equal between these two communities, the latter would be considered the more diverse because its evenness is greater.

Species richness of gastropods in the Luquillo Mountains appears to be relatively unaffected by hurricanes.

increasingly dominated by a few common species. Nevertheless, it does not appear that these species out-compete the rarer species or have other negative effects. Instead, it seems that populations of those species simply grow most rapidly and show the most obvious effects of hurricanes because of their high abundance and ease of capture.

The spatial distribution of species was most random and patchy immediately after hurricane disturbance and grew more predictable over time. This has implications for the abundance and diversity of gastropods. As time passes



Gaecotis nigrolineata



Cepolis squamosa



Stream running through El Yunque. (Photograph by Jason Lech).

regime will change in coming decades. Debate continues about whether increasing ocean surface temperatures will lead to increased frequency of intense hurricanes, but it is well established that average air temperatures are increasing in northeastern Puerto Rico, driven both by global warming trends and rapid urbanization, and that average annual precipitation is declining. Although gastropod populations seem remarkably resilient towards cyclical natural disturbances, it remains to be seen how they might be affected

by long-term changes in climate or by increased disturbance frequency.

My ongoing research efforts build on these observations. First, I continue to monitor gastropod abundance and diversity on the long-term study plots, to watch for long-term environmental change that might be associated with urbanization or climate change. Second, I am developing collaborative projects that will examine functional links between gastropods and other organisms in the Luquillo Mountains. For example, Dr. Jenna Mendell, her

student Jennifer Conway, and I are investigating the composition of the bacterial community that inhabits the intestine of a common snail species, *Pleurodonte caracolla*. This will provide insight into how these highly herbivorous snails are able to process hard-to-digest plant compounds and contribute to decomposition of leaf litter. Also, in collaboration with Dr. Craig Zimmermann of Rogers State University, I have established an experiment to test how snail shells, which provide large, concentrated sources of calcium, affect soil characteristics and leaf litter composition. Ultimately, these ongoing projects will build on past results while broadening the context and applicability of my work and facilitating more robust predictions of how tropical forests will respond to changing disturbance regimes and increasing human activity.

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Megalomastoma croceum



Alcadia striata