



Metabolic energy density reveals biodiversity-related differences in resilience to disturbances in longleaf pine ecosystems

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Changes in climate and other human-induced disturbances have become more frequent and severe over recent decades. Yet we still lack predictive power about how an ecosystem's structure and function will be altered by perturbations, and how ecosystems adapt to change. Ecosystems exhibit varying responses to disturbance, demanding a unifying metric to assess resilience that accounts for these complex and dynamic feedbacks. Our study introduces a framework to quantify energy utilization of ecosystems through the application of thermodynamic laws. It gives us a theoretical basis to quantify ecosystem resilience using fundamental metrics of energy density, improving traditional methods to identify resilience based on ecosystem productivity or entropy.

We investigated the role of metabolic energy density to quantify resilience to environmental perturbations in longleaf pine (*Pinus palustris* [Mill.]) savannas with different levels of biodiversity owing in part to anthropogenic legacy. We utilize three sites (mesic, intermediate, xeric), and 24 site-years of eddy covariance and soil respiration measurements. Agricultural practices at the intermediate site resulted in lower biodiversity, in contrast to the more biodiverse mesic and xeric sites. We calculated available energy from gross ecosystem exchange of CO₂ and its dissipation into metabolic energy density, such as energy used for the recycling of Adenosine Triphosphate, biomass production and plant metabolism. We hypothesized that 1) More resilient sites conserve more resources and will have higher metabolic energy density compared to other sites, as a function of their legacy; and 2) Sites which are further along a successional stage will have a higher adaptive capacity to disturbance, by lowering their energy density more rapidly, compared to less resilient sites.

We show that sites with higher biodiversity rapidly adapted to disturbances by lowering metabolic energy densities by nearly 20%. In contrast, the site that experienced higher levels of anthropogenic modification regularly exceeded available energy, which decreased its resilience, as no energy storage was available when resource availability was low. Stored energy resources – for example via non-structural carbohydrates (NSCs) – were used at this site during approximately 20 months over the 8 year study, while this was necessary during less than 5 months at the more resilient sites with higher biodiversity. This resulted in slower acclimation to drought at the intermediate site. These ecosystem responses were not apparent using metrics of carbon dynamics, and highlight the critical role of measuring or estimating energy flux into different plant components (such as NSCs) for a comprehensive understanding of ecosystem metabolism. We conclude that sites that matured with natural environmental variability developed strategies to adapt to disturbances by conserving energy; whereas anthropogenically altered sites used energy less effectively, and thus showed lower adaptive capacity.

Our results could have large impacts for present and future ecosystem management given that humans have altered most global ecosystems. Our study supplies the tools and knowledge for forest property managers, as well as conservationists, to identify sites that are more vulnerable to disturbance events, which could significantly lower the costs for site management to maintain necessary ecosystem functions.