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Ecosystem capacitance: an integrative buffer against disturbance

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1 Introduction

When drafting a research article (Gough et al., 2021), I was at a loss for a term that describes the status of the ecosystem-wide resource base *before* disturbance that could help buffer against changes in forest functioning *during and after* disturbance. The concept of “material and information legacies”, summarized by Johnstone et al. (2016), describes the biotic and abiotic resources, including the “information” encoded in genes, that are retained through disturbance and which aid in the recovery of community structure and ecosystem functioning. Such legacies include retained biomass, nutrients, seeds and other propagules, and adaptive traits that pass through a “disturbance filter”, supporting recolonization, regrowth, and the recovery of biological and genetic diversity. But, what term conveys the status and quantity of these functionally-relevant resources prior to disturbance?

The answer: forest ecologists and managers have no agreed-upon term to describe the status of disturbance-buffering materials before disturbance occurs, even though the abundance and diversity of biotic and abiotic resources before disturbance influences how ecosystems respond to droughts and extreme weather, insect pests, pathogens, and fire (Burton et al., 2020). For example, forests depleted in nutrient capital, biological and genetic diversity, seed supply, and plant biomass before disturbance are more prone to significant changes in structure and function when disturbance occurs (Hughes and Stachowicz, 2011; Kranabetter et al., 2016). Moreover, the material and information legacies that persist through disturbance are partly dependent upon the resource base prior to disturbance, with more frequent and severe disturbances progressively eroding stored resources (Latty et al., 2004).

2 Ecosystem capacitance as an indicator of disturbance buffering capacity

Modifying century-old terminology used by physicists and engineers and, more recently, plant physiologists, I propose the use of “ecosystem capacitance” to describe the status of stored biotic and abiotic materials available to sustain or support the recovery of systems-level functioning *before* disturbance occurs. Broadly, “capacitance” refers to stored energy or mass that, when mobilized, buffers against systems-level change. Originally referencing the storage of electric charge, plant physiologists use capacitance to describe the quantity of stored water within tissues (Bryant et al., 2021) and ecosystems (Konings et al., 2021), a resource that can be remobilized to stabilize water transport thorough stems and into the atmosphere (i.e., transpiration) during periods of drought.

Pivoting from its original definition, “evolutionary capacitance” describes accumulated genetic variation within a population, which, under stressful conditions, may be crucial to adaptation and population persistence (Bergman and Siegal, 2003).

The adoption of such terminology has benefits because, like metrics of ecological stability borrowed from physics, ecosystem capacitance could be quantified and, therefore, serve as a diagnostic measure of an ecosystem’s capacity to buffer against or reduce disturbance-driven changes in structure and function. Concepts and terminology borrowed from physics and engineering are not new to ecology. Electrical resistor diagrams have been used by plant physiologists for decades to map and model how water moves from soils through plants and into the atmosphere (Luo et al., 2013). More recently, conceptions and calculations of ecosystem stability, which encompass several component parts, including resistance and resilience, borrow heavily from engineering principles to describe and quantify structural and functional changes in response to disturbance (Hillebrand et al., 2018).

3 Discussion and application to forest management and disturbance mitigation

For forest managers, ecosystem capacitance could serve as an indicator of the *potential* to sustain or recover functioning, and goods and services after disturbance. Similar to ecosystem

health indicators (Shear et al., 2003), a systematic but tailored accounting of ecosystem capacitance could inform conservation and management goals that aim to sustain or recover targeted goods and services following regionally-forecasted disturbance events. In this context, the biotic and abiotic materials assessed to derive ecosystem capacitance would be system- and disturbance-dependent, and consider which resources most limit the functions, goods, or services of interest. For example, in accordance with the “insurance hypothesis”, high biological, functional, and genetic diversity alone may reduce temporal variation in wood production and carbon sequestration during drought and in response to extreme weather (Mori et al., 2013; Morin et al., 2014), but additional accounting of plant biomass and nutrient capital may be critical if the goal is maximizing rates of forest carbon sequestration. The factors underlying ecosystem capacitance also will vary by forest type because principal limiting resources (Running et al., 2004) and prevailing disturbance regimes (Cohen et al., 2018) differ substantially among forest biomes and plant functional types (Amiro et al., 2010). For example, water is a primary limiting resource in evergreen needle leaf forests of western North America, where insects and fire are prominent disturbances (Masek et al., 2013). In contrast, temperate deciduous forests in eastern North America range from nitrogen-limited to nitrogen-polluted (Vitousek et al., 2022), and are more susceptible to insects, pathogens, and wind throw (Fischer et al., 2013; Flower and Gonzalez-Meler, 2015). Extending the diversity-focused insurance hypotheses, indices of ecosystem capacitance

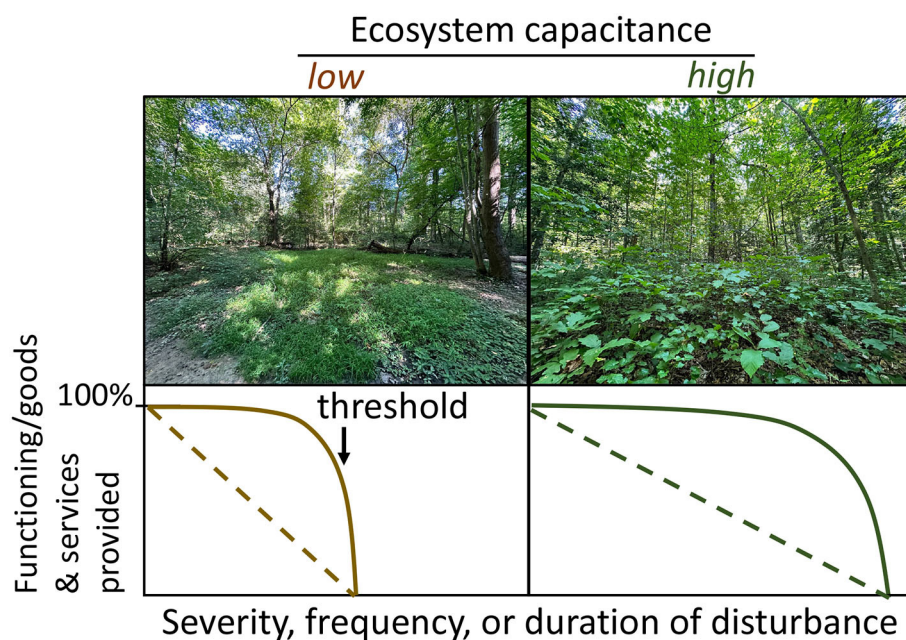


FIGURE 1

Temperate deciduous broadleaf forests with contrasting low and high *ecosystem capacitance*, respectively. The ecosystem on the left is depauperate of indigenous plant biodiversity, mid-canopy plant biomass, and soil organic matter, resources that are crucial to sustaining a number of functions—from wood production to nutrient retention—during and after insect pest and pathogen outbreaks or drought, disturbances that are increasingly common in temperate deciduous broadleaf forests. The high capacitance ecosystem on the right, contrastingly, has abundant stored resources and is expected to exhibit less or delayed functional change as disturbance severity, frequency, or duration increases. In both cases, ecological theory and observations suggest declines in ecosystem goods and services with increasing disturbance severity, frequency, or duration could proceed linearly (dashed line) or non-linearly.

would ideally encompass and integrate all quantifiable abiotic and biotic properties that strengthen ecosystem stability in the presence of disturbance (Running et al., 2004; Cohen et al., 2018; Vitousek et al., 2022). While the factors contributing to ecosystem capacitance will differ among forests, the conceptual relationship between capacitance and ecosystem goods and services is the same: across a continuum of disturbance severity, frequency, or duration, forest ecosystems with low capacitance are expected to exhibit a loss of function more rapidly or at lower disturbance thresholds than ecosystems with high capacitance (Figure 1).

Developing tractable approaches for quantifying meaningful measures of ecosystem capacitance will require dialogue and collaboration among forest scientists and managers, akin to the iterative process that led to practitioner- and policy-relevant wetland assessment approaches and measures (Herlihy et al., 2019). Assessments of wetlands, similarly motivated by ecological restoration and sustainability goals, were developed through long-term partnerships among researchers, practitioners, and policy makers. With standardized wetland assessment protocols in wide use, these tools provide intercomparable data-driven and evidence-based diagnostics with which to guide preemptive and adaptive management, while employing methods and providing metrics that are accessible and meaningful to managers (Maltby, 2022). Indeed, national forest inventories, such as the United States Department of Agriculture's Forest Inventory and Analysis, report a suite of longitudinal data that could be used to develop quantitative indicators of ecosystem capacitance, including tree crown conditions, stand biomass, tree mortality, and forest composition (Woodall et al., 2011). Moreover, such ground-based inventories provide crucial assessments of ecosystem functioning and goods and services, including carbon sequestration and timber production. When paired with increasingly available remotely-sensed data describing the physical arrangement and taxonomic diversity of vegetation within forest canopies, inventory data provide a rich complementary dataset with which to develop and test the efficacy of ecosystem capacitance as an indicator of preparedness against future disturbance.

Do we need another term in the already extensive glossary of forest ecology? Possibly not, but the conceptual and quantitative frameworks used to characterize, predict, and interpret the effects of disturbance on forest biodiversity, structure, function,

goods and services remain unsettled (Müller et al., 2023). With global change-related disturbances increasing, the standardization and maturation of language and concepts that forest ecologists and managers use to describe, predict, mitigate, and measure disturbance effects on ecosystems is, arguably, more important than ever.

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CG: Conceptualization, Writing – original draft.

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