# Ecosystem Entanglement and the Propagation of Nutrient-Driven Instability

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## Abstract

Almost 50 years ago, Michael Rosenzweig pointed out that nutrient addition can destabilize food webs, leading to loss of species and reduced ecosystem function through the paradox of enrichment. Around the same time, David Tilman demonstrated that increased nutrient loading would also be expected to cause competitive exclusion leading to deleterious changes in food web diversity. While both concepts have greatly illuminated general diversity-stability theory, we currently lack a coherent framework to predict how nutrients influence food web stability across a landscape. This is a vitally important gap in our understanding, given mounting evidence of serious ecological disruption arising from anthropogenic displacement of resources and organisms. Here, we combine contemporary theory on food webs and meta-ecosystems to show that nutrient additions are indeed expected to drive loss in stability and function in human-impacted regions. However, this loss in stability occurs not just from wild oscillations in population abundance, but more frequently from the complete loss of an equilibrium due to edible plant species being competitively excluded. In highly modified landscapes, spatial nutrient transport theory suggests that such instabilities can be amplified over vast distances from the sites of nutrient addition. Consistent with this theoretical synthesis, the empirical frequency of these distant propagating ecosystem imbalances appears to be growing. This synthesis of theory and empirical data suggests that human modification of the Earth's ecological connectivity is "entangling" once distantly separated ecosystems, causing rapid, expansive, and costly nutrient-driven instabilities over vast areas of the planet. The corollary to this spatial nutrient theory, though – akin to weak interaction theory from food web networks – is that slow spatial nutrient pathways can be potent stabilizers by moderating flows across a landscape

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