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Pathogen impacts on forest diversity: inferring the combined impacts of all pathogens on all hosts, with environmental context

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Ecologists hypothesize that species-specific pathogens promote forest diversity by preferentially attacking tree host species whenever they become abundant. By disproportionately reducing the success of dominant tree species, pathogen attack helps insure that rare species are not driven to extinction by their abundant competitors. It has not been possible to test this hypothesis, in part because pathogen effects are difficult to detect and they could interact with environmental variables and with other species. We used an experimental approach to test for environmental factors that could affect pathogen incidence, infection, and host survival. Infection is documented by pathogen cultures and by nuclear ribosomal DNA sequencing.

We discuss how hierarchical models can be used to infer the combination of factors that influence incidence of pathogens and their effects, individually and together. An important advantage is the capacity to model all pathogens and all hosts in a single analysis, allowing for environmental influences at multiple stages. In this way, all hosts provide evidence for pathogen incidence, and pathogen impacts on hosts can be examined in the context of the full pathogen load. A causal graph includes i) pathogen incidence, which depends on moisture, ii) host-plant infection, which depends on different infection rates of each pathogen, iii) pathogen-specific detection probabilities, and iv) host survival, which depends on all pathogens, moisture, and light availability. Detection and survival are taken as known, but detection data are limited to a subset of sampled individuals. Pathogen incidence is partially known; it is known for those plots where any plant tests positive for the pathogen, but unknown for all other sample plots. Infection status is inferred.

We show how a traditional model gives misleading results, and how hierarchical modeling can provide improved insight. Because both pathogens and hosts grow and survive better at high moisture and high light levels, incidence and infection

rates increase with resources, but host survival also improves. By modeling the relationships in stages, including all hosts and pathogens together, we show that pathogens continue to have a detrimental effect on host survival at high resource levels, despite the fact that hosts do better. We do not infer the host specificity needed to implicate pathogens as factors promoting forest diversity.