Forest Tree Species Diversity Depends on Individual Variation

February 25 2010

Elevation contours outline tree heights, allowing for research on effects of light on the forest. Credit: James Clark

(PhysOrg.com) -- It's a paradox that's puzzled scientists for a half-century. Models clearly show that the coexistence of competing species depends on those species responding differently to the availability of resources. Then why do studies comparing competing tree species draw a blank?

Competitors like black gums and red maples have coexisted for millennia in the shaded understories of eastern U.S. forests, yet species-level data offer scant proof that they respond differently to environmental fluctuations that limit access to light, soil moisture and other essential resources.

These are the very differences required for their long-term coexistence. Are the models and theory flawed? Or is it the data?

A paper in this week's issue of the journal *Science* offers new insights that may resolve the puzzle.

"Species differences do exist, consistent with theory, but species-level data don't show them," says forest ecologist James Clark of Duke University, the paper's author. In order to see them, he says, you have to go to the individual level.

"Scientists working to address pressing ecological issues, such as the spread of invasive species, will benefit from this finding," says Todd Crowl, program director in the National Science Foundation (NSF)'s Division of Environmental Biology, which funded the research.

Species-level studies--the preferred approach in nearly all past research on forest tree diversity--rely on average responses from sample populations to infer information such as average growth, reproduction and survival rates for entire species over time.

They're useful for many purposes, Clark says, but because they assess species' responses in only the handful of environmental dimensions that can be measured, they miss most of the subtle ways in which species differ.

"The environment varies in thousands of ways," he says. "Species can differ in how they respond in all these dimensions, and we can only measure a few of them."

Failure to find tradeoffs in how species respond in the few measurable dimensions, such as the ability to survive in a shaded understory versus growing fast in full sunlight, has promoted a false view, according to

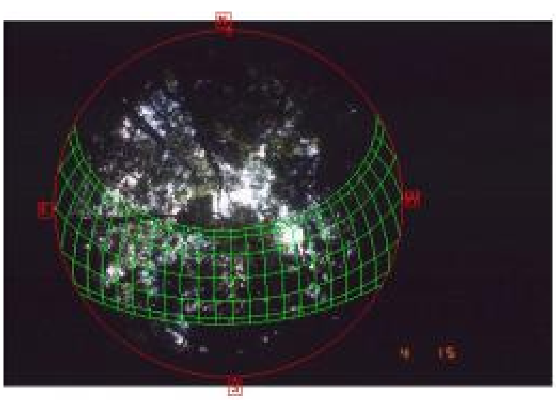
Clark.

"Looking at only a handful of averaged responses in a few dimensions may lead to the conclusion that all species react more or less the same," Clark says.

He analyzed more than 226,000 "tree years" of data from more than 22,000 individual trees of 33 species. The trees are in 11 forests in three regions of the U.S. Southeast, including NSF's Coweeta Long-Term Ecological Research (LTER) site.

Coweeta, in the eastern deciduous forests of the southern Appalachian Mountains, is one of 26 such NSF LTER sites.

In his study, Clark estimated annual rates of growth, fecundity and survival risk for every tree in the 11 stands from observations of tree diameter, canopy spread and height, reproductive status, survival, and seed dispersal.



An alternate look at a forest: through a grid in which individual trees may be seen. Credit: Jim Clark

He quantified variations between individuals within populations over time spans ranging from six to 18 years.

His painstaking analysis revealed none of the tradeoffs postulated for trees in species-level averages.

"Individuals are responding in many dimensions in different ways, but with more similarity to other individuals of the same species than to individuals of different species," Clark says.

That's important, he explains, "because as the individuals in a population react to the environment, the similarity they share with others of their own species tends to concentrate competitive pressure within species. The tendency to compete within species allows multiple species to share the landscape."

These findings, he notes, are consistent with the ecological theory that coexistence of competitors requires stronger competition within than between species.

The change in perspective yields new insights into a variety of pressing ecological issues.

"We've always wondered, for instance, how introduced species could invade existing communities where competition is already intense," says Clark. "The assumption was: since existing species are competing for limited resources, it must be especially difficult for invaders to come in, establish and compete successfully.

"But these results suggest that competitive exclusion doesn't work as well as we thought. Knowing that diversity is likely controlled by variations in many dimensions makes it easier to understand why invasions are so common--and suggests new ways of thinking about why they are so successful."

Provided by National Science Foundation