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Variation in the soil template drives large variation in forest functioning, composition, and structure during tropical dry forest secondary succession

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Observations of tropical forests have revealed large variations in aboveground biomass, plant composition, ecosystem structure, and biogeochemical functioning across plots. A relatively large amount of variability remains even when precipitation and stand age are controlled for. Here, we analyze the extent to which variability in ecosystem processes and characteristics can emerge from solely from variation in the soil template. We performed controlled experiments using a mechanistic, numerical model. The model dynamically couples ED2 (vegetation dynamics), MEND (biogeochemistry), and N-COM (plant-microbe competition for nutrients). Here, the MEND-component of the model has been extended to include nitrogen and phosphorus cycles. We focus on simulation of eighteen 0.1-hectare forest inventory plots in Guanacaste, Costa Rica that were established in 2008. All plots experience statistically similar climate conditions, but vary greatly in terms of soil texture, soil percent carbon (C), carbon-to-nitrogen (N) ratios, extractable phosphorus (P), total P, and other soil properties. We predicted that our simulations would show that (1) ecosystem-level state variables would vary between the plots because of differences in nutrient limitation, (2) because of non-linearities in nutrient cycling, a single simulation forced with average soil conditions would differ from the average of the eighteen simulations that resolved variability in the soils, (3) because different plant functional types (PFTs) have different nutrient requirements, variation in the soil template would lead to variation in PFT composition.

These three predictions were confirmed by model simulations. After 40 years of secondary succession, the spread in plant biomass was about 40% of the mean. The accumulated biomass was positively correlated with the initial amount of non-occluded soil P. Ecosystem structure also varied, with the height of the centroid of leaf area index (LAI) also being correlated to non-occluded soil P. A simulation with artificially large N and P deposition rates had a much smaller spread in accumulated aboveground biomass, confirming a nutrient limitation dynamic. A single simulation forced with average soil conditions generated yielded about 10% more aboveground biomass than the average of the 18 simulations. The proportional amounts of different PFTs simulated in the different plots also varied widely and depended on differing degrees and N and P limitation. Overall, our simulations provide a mechanistic link between realistic variations in the soil template and large variation in ecosystem functioning, composition, and structure during secondary succession. Because of these strong linkages between the soil template and emergent ecosystem characteristics, we suggest that the grid structure of regional and global models better account for variations in the soils.