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## Considerations of Scale and Ecological Processes in a Forest Migration Model: A Reply to Roth

Roth (1996) offers many suggestions intended to give a more sound "ecological grounding" to the migration model that I presented (Dyer 1994). Before addressing her comments, it may be useful to place the model in context with earlier works. Studies that have explored the potential impacts that climatic warming might have on North American forest communities traditionally have employed one of two general methodological approaches: climate-range correlation, or forest stand simulation models.

Climate-range correlation studies assume that present-day vegetation is in equilibrium with climate and determine the value of key climatic variables that are coincident with the current range limit of particular species; the correspondence is presumed to indicate a climatic constraint on the species distribution. Once climatic correlates are assigned, the consequences of a climatic warming on species distributions are assessed by delimiting geographic displacement of the presumed climatic control under global warming scenarios. Climate-range correlation studies allow examina-

tion of potential vegetation changes at a continental scale (e.g., Overpeck et al. 1991; Davis and Zabinski 1992). Researchers employing this approach would not argue that the present correlation of distributions with climatic variables "ensures that these are the sole or primary factors governing biotic ranges" or assume that "ranges will shift predictably in response to climatic change" (Roth 1996, 84). Nevertheless, since past climate changes have resulted in species migrations, and given our limited understanding of large-scale vegetation dynamics, it is logical to argue for the primacy of climate in defining plant ranges at broad spatial scales.

Forest stand simulation models are mechanistically oriented computer programs that calculate annual establishment of new seedlings, growth of extant trees, and mortality on a small plot. Community dynamics are based on plot conditions, and implicitly account for competition for light, water, and nutrients among the trees. Once forest simulation models have been calibrated for current climatic conditions, the parameters that govern species

regeneration, growth, and mortality are modified to reflect projected future climate conditions, and the model run continues (e.g., Davis and Botkin 1985; Overpeck et al. 1990). This process-oriented approach requires a smaller scale of analysis, and modeled plots are usually less than 1 ha.

The aim in presenting my migration model was to provide a preliminary link between the two traditional approaches, by examining dispersal (absent in climate-range correlations) over extensive geographic areas (precluded in forest stand simulation models). The ability to bridge spatial scales is a critical gap in our examination of global change.

My article described part of a larger project exploring forest migration in response to global warming (see Dyer 1995). In this project I modeled two trees with different life-history traits: a bird-dispersed species and a wind-dispersed species. Loblolly pine was used to parameterize the wind-dispersed species because its economic importance has prompted studies of its life history characteristics. The results generated by the model were not intended to serve as predictions of a specific tree's response to climate warming, but rather to indicate that a wind-dispersed species may be unable to track its changing range limits, due to the rapidity of warming relative to its dispersal abilities coupled with habitat fragmentation.

I agree with Roth that the model does not explicitly include life history traits pertinent to dispersal and establishment. It was not my intention to model succession on the two 22,500 km<sup>2</sup> study areas or "plots," but to examine the potential movement of a tree species through real-world landscapes containing human-induced obstacles. This objective requires a different scale of analysis to model dispersal and colonization than that used to model succession on a given plot. Although specific values and assumptions used in the model are open to question, Roth rightfully assumes that I sought to maximize seed production and dispersal to avoid being "falsely alarmist"; since modeled migration rates still fall well short of projected shifts in the species climatic range, I do not think I am offering "reassuring predictions" either (Roth 1996, 84).

The resolution of the land use data also placed constraints on the model. Roth states (p. 83) that "successful invasion of undisturbed

hardwood forests by [loblolly pine] is . . . questionable." This does not accurately reflect the definitions of the Land Use Land Cover (LULC) classes. "Forest lands" are not necessarily old-growth hardwood forests. The U.S. Geological Survey defines forest lands merely as having 10% or more of tree-crown canopy closure (Anderson et al. 1976). In addition, although the LULC maps are comprised of 4 ha cells, forested stands less than 16 ha on the original air photos, from which the maps were prepared, are not even represented (thereby masking much landscape heterogeneity at the "ecological" scale). This definition would not necessarily preclude successful invasion by a shade-intolerant species.

Roth also states that fragmentation may actually benefit the establishment of a shade-intolerant species such as loblolly pine. Perhaps a clarification of my usage of the term "fragmentation" should be stressed. My reference to "barriers to dispersal caused by habitat fragmentation" (Dyer 1994, 456) was in regard to human-disturbed, non-forest land use isolating forest land, not to "gaps" in closed forests or along forest edges. Based on the LULC characteristics of the two study areas, non-forest lands would not appear to offer a suitable alternative for establishment of loblolly pine. Along with "forest lands," "urban" and "agriculture" land uses comprise 98.90% of the Appalachian study site and 93.34% of the Coastal Plain study site (Dyer 1994, Table 1). Urban areas are characterized by intensive use with much of the land covered by structures, and agricultural land is used primarily for production of food and fiber (Anderson et al. 1976). Thus, although these land uses may offer suitable microenvironments for the establishment of shade-intolerant tree seedlings, it is unlikely that land use practices on these lands would allow successful colonization. Although Roth implies that the possible migration of loblolly pine may be favored by the abandonment of agricultural land as it has in the past, in the model land use is static. My intention was to accurately capture real world land use patterns. Although there is little doubt that land use patterns will change in the event of a climatic warming, it is impossible to accurately project future land use change (such as agricultural land abandonment); to do so would have added yet more uncertainty to the model. I do not

believe, therefore, that it is untenable to assume that the modeled tree species' potential migration rate is correlated with the percentage of forested area in the two study areas, as Roth contends.

The overriding criticism offered by Roth throughout her commentary is that the model should be more "ecological." Based on her comments, the model ideally should monitor the position of individuals of *all* species on each 4-ha cell, their age, growth, density, and position in the canopy, in order to assess the role of competition, to insure that seed trees are the dominants or codominants of the stand, and to guarantee pollination. (In essence Roth is advocating a "forest stand simulation model" approach.) Complicating factors that Roth mentions include the ability of extant trees to adapt to changes in climate, differential responses to CO<sub>2</sub> enrichment, altered decomposition rates in a warmer climate, changes in disturbance regimes, and changes in land use practices brought about by climate change. Other factors she feels are critical to the model include depth and composition of litter, seed predation, and direction of the prevailing winds at the time of seed release in a future warmer world. A multitude of scenarios would need to be performed if these factors were to be included, given the potential variability of response and the uncertainty of predicting responses under future climatic conditions.

I agree with Roth that the inclusion of these factors, if it were possible, would greatly improve the model's realism. In fact, there are many more factors that I could add, some of which may be more critical than many in her list. However, I think Roth fails to acknowledge the fundamental constraints of scale and resolution in this geographical problem. The two 150 km × 150 km study sites are divided into grid cells measuring 200 m on a side (4 ha), such that each study area contains 562,500 cells. It is not computationally tractable at this time to propose linking this many study plots in a forest stand simulation model approach. As Roth states (p. 84), "it would be absurd to expect a model to incorporate the full range of ecological detail impinging on the migration of even one species."

Although the impulse is to focus on smaller-scale effects using a "bottom-up" approach, in

order to proceed from forest stand simulation models to larger scales it likely will be necessary to reduce the number of variables included in any model. Although I plan to include additional factors in subsequent model versions, I believe dispersal ability and land use pattern are two of the most critical factors. If a species cannot reach new habitat, or if suitable habitat is unavailable, the other factors become moot. To determine which biotic and abiotic factors are most crucial to understanding migration at broad spatial scales, it will be necessary to draw upon continuing research employing process-oriented forest stand simulation models, paleoecological reconstructions, and field experimentation. ■

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