Ecological Insights from Long-term Research Plots in Tropical and Temperate Forests

Organized Oral Session 40 was co-organized by Amy Wolf, Stuart Davies, and Richard Condit, and held on 6 August 2009 during the 94th ESA Annual Meeting in Albuquerque, New Mexico.

An International Network of Forest Research Sites

This session was devoted to findings from an international network of long-term forest dynamics plots, providing some of the first comparisons between the tropical and temperate study areas. Whereas most ecologists recognize the importance of long-term research (Callahan 1984, Likens 1989, Magnuson 1990, Hobbie et al. 2003, and others), large-scale projects like this one are rare. The global network of *forest dynamics plots* has expanded since its origin in the early 1980s, yet research at the plots has remained integrated due to a combination of individual scientists' efforts and institutional commitments from the Center for Tropical Forest Science (CTFS, ‹www.ctfs.si.edu› of the Smithsonian Tropical Research Institute and the Arnold Arboretum of Harvard University (Hubbell and Foster 1983, Condit 1995). Today, 26 large plots have been established in tropical or subtropical forests of Central and South America, Africa, Asia, and Oceania, along with 8 recently added temperate forest plots. A standard protocol (Condit 1998) is followed at all sites, including the marking, mapping, and measuring of all trees and shrubs with stem diameters ≥1 cm.

An underlying objective of the ESA session was to illustrate how an understanding of forest dynamics can contribute to long-term strategies of sustainable forest management in a changing global environment. Stuart Davies, Director of the Center for Tropical Forest Science, opened by describing the current plot network and the pivotal role of CTFS in supporting research at sites in 20 countries. Since the establishment of the first plot at Barro Colorado Island in Panama in 1980, researchers have applied the standard field methods in plots covering >1200 ha (12 km^2). Field teams have measured ~3.5 million living trees belonging to at least 7900 species. Not only has this ambitious effort led to important ecological insights, but the network continues to build expertise and research capacity in the countries where research is being conducted. New sites continue to be added, and not a single forest dynamics plot has discontinued the monitoring protocol.

Davies summarized some of the important published findings from forest dynamics plots. In the tropics, tree species diversity decreases with length of the dry season and insularity. Dispersal limitation, niche differences, and density dependence all have been demonstrated at forest dynamics plots, even though neutral dynamics can successfully predict species relative abundance distributions. In fact, most species (49–74%) in all of the forest dynamics plots exhibit some degree of habitat specificity. These attributes are especially important predictors of long-term vegetation change. Floristic changes on Barro Colorado Island, for example, have shown a consistent trend toward increased drought tolerance and increased average wood density. The baseline data established at these and other sites will continue to provide vital information about the effects of climate change and environmental perturbations.

Stephen Hubbell, co-founder of the first forest dynamics plot with Robin Foster and others, described how different scales of reference reveal different types of ecological processes. Density and frequency-dependent interactions are strong at local spatial scales, but they become weak at intermediate scales. Hubbell introduced a new theory, the Enemy Susceptibility Hypothesis, which might explain an unexpected pattern of negative spatial autocorrelation of species' population growth rates (r) at large (>700 m) spatial scales. This pattern is especially strong among rare species. He proposed that pathogens play an important role in keeping rare species rare by preventing them from becoming locally common anywhere. A video simulation demonstrated the complex spatial dynamics of pathogen–host interactions, illustrating the important geographic effect of pathogens on host communities.

Jerry Franklin provided an historical perspective on long-term forest research plots and their critical role in testing predictions of ecological models and theories. He and co-authors have been monitoring permanent plots in North America's Pacific Northwest for >50 years, but Franklin asserted that neither regional networks like these nor the current system of forest dynamics plots are yet adequate to address major issues of ecological theory or environmental change. A sustained international system of large, permanent forest research plots will pay important dividends in understanding forest ecology and human impacts on the environment. Institutional and government support are necessary to sustain a network of permanent research sites, but commitments by individual scientists and a culture of effective mentoring will be equally important ingredients of success.

Robert Howe, Amy Wolf, and Richard Condit described results from one of the first forest dynamics plots in the temperate zone (Wisconsin, USA), where species diversity is more than an order of magnitude lower than at equivalent-sized forests in the humid tropics. Despite the simpler community structure,

patterns of species abundance are not unlike those in tropical forests, and many of the same processes (geologic history, local disturbance, habitat specialization, interspecific competition, and dispersal constraints) influence species distributions. As in tropical forests, most species in temperate forest plots are rare, maintained by dispersal from the surrounding metacommunity. The pattern of relative species abundances in the Wisconsin forest dynamics plot closely follows the log-series distribution, as predicted for tropical forests by Hubbell's zero-sum neutral theory. This result is obtained despite the clear existence of species interactions and niche differentiation.

Keping Ma, Director of the Institute of Botany at the Chinese Academy of Sciences, and coauthors described the newly established network of four large forest dynamics plots in China, ranging from a high-latitude temperate forest in Jilin Province in the northeast to species-rich subtropical forests in southern Yunnan Province. Research at these sites has resulted in 16 peer-reviewed publications during the past three years, including studies of spatial tree distribution patterns, species–area relationships, conservation genetics, dispersal dynamics, and habitat associations. Major findings include evidence of density dependence in 83% of subtropical tree species after the effects of habitat heterogeneity have been removed; a trend of decreased aggregation of trees with increased scale of reference; and the implication of multiple factors (dispersal and habitat heterogeneity) in species–area relationships. Ma also described the Beijing Living Herbarium Project, which uses digital photography to document plant species occurrences at long-term research sites across China.

Sean Thomas, Michael Drescher, and Rajit Patankar outlined the scientific rationale for large-scale forest plots. These plots create a research platform that efficiently addresses many questions within a spatial scale that is highly relevant to important ecological processes. Some problems or questions can be addressed at a regional scale (e.g., parameterization of individual-based forest simulation models, analysis of diversity–productivity patterns), while others are made possible by the existence of a global network of plots (e.g., are natural enemy effects weaker in temperate than tropical forests?). Thomas and coauthors described findings from their recently established temperate forest plot in Ontario, Canada, including the documentation of canopy thinning in old/large trees, the strong effects of topography and stem density on species richness, and the ecological importance of maple spindle gall mites in forests dominated by sugar maple (*Acer saccharum*).

Permanent forest dynamics plots have become an important resource for global studies of carbon dynamics, including a research program led by Helene Muller-Landau and numerous Center for Tropical Forest Science (CTFS) colleagues. Forests contain ~38% of terrestrial carbon pools and account for 48% of terrestrial net primary production, so an understanding of carbon dynamics in forests is critical for understanding global carbon cycles. Muller-Landau's presentation illustrated that forest carbon pools are dynamic, varying spatially and temporally in response to climate, species composition, and other factors, including human impacts. Research at forest dynamics plots provides important information about carbon stocks, carbon dynamics, and mechanisms that underlie variation in carbon pools and fluxes. On Barro Colorado Island in Panama, for example, soil contributes 60% of measured forest carbon stocks, trees 36%, woody debris 3%, and lianas <1%. Initial results of the carbon studies by

Muller-Landau and others have revealed extensive variation in tree carbon stocks within and among tropical forests. Species composition, which is likely to be modified in response to human-induced climate change, plays a significant role in explaining this variation. The forest dynamics plots provide a detailed baseline for understanding long-term changes in forest carbon storage, information that will be critical for understanding the impacts of global change.

Richard Condit described simulated tree communities, starting with real spatial configurations of trees in the Korup (Africa) and Barro Colorado Island (Panama) forest dynamics plots. The neutral ("voter") model of Hubbell leads to conspicuously different species distribution patterns depending on the mean dispersal distances of species. Short dispersal distances (10 m) lead to highly aggregated distributions, whereas longer dispersal distances (>200 m) lead to more random distributions in the absence of niche segregation or species' habitat preferences. If niche segregation among species is incorporated into the models, similar results are obtained, except that distributions are predictably aggregated around favored microhabitats. Condit compared simulations representing different underlying community dynamics (different dispersal distances and different degrees of niche differentiation) with actual patterns observed in tropical forest dynamics plots. Invariably, observed patterns matched simulations with high degrees of species input through dispersal. These findings strongly suggest that species assemblages in forest dynamics plots (15–50 ha) are influenced significantly by species input from the surrounding metacommunity. A high proportion of species in these assemblages might be maintained by persistent immigration, not by niche differentiation among coexisting species. Condit's approach provides insights into the processes that structure tree communities, and additionally suggests the scale at which dispersal occurs in these tree communities. In most cases, dispersal distances of at least 100–200 m are prevalent.

One of the first and perhaps most dynamic permanent plots is the Mudumalai Forest Dynamics Plot in southern India described by R. Sukumar, H.S. Suresh, and H.S. Dattaraja. This dry tropical forest experiences periodic fires, annual droughts, and disturbance by elephants, resulting in dramatic changes in the abundance of grasses and small-stemmed woody plants. Despite high disturbance rates, the composition of canopy trees has been remarkably stable, with mortality rates below or equal to that of canopy trees in tropical moist forests. During >20 years of annual forest monitoring, Sukamar and colleagues have found no evidence that current frequencies of fire and large-mammal herbivory (including one of the highest elephant densities in the world) will convert the Mudumalai forest to savanna or grassland. Fire and drought impose short-term changes in the vegetation, particularly understory grasses and tree recruits, but carbon stocks have remained quite uniform and overall community properties have not shifted dramatically over the long term. Studies from Mudumalai clearly illustrate the value of long-term forest monitoring and the complexity of ecological responses to environmental change.

Research in this growing network of permanent forest plots has provided not only baseline data for regional and global ecological comparisons, but it has also provided a fertile platform for generating new ideas about the structure and dynamics of forest communities. In addition to this Oral Session, more than 60 other papers and posters were presented at the ESA Meeting in Albuquerque from researchers associated with the forest dynamics plot network. The capacity audience at this organized oral session suggests that interest in coordinated international research on forests is high. Such interest is likely to grow as more sites are added to the network and as the data accumulating from systematic, long-term monitoring continues to address critical issues for the future of the world's forests.

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