SPECIAL FEATURE

Agroforests as Model Systems for Tropical Ecology[1]

Not too long ago, many ecologists looked askance at research conducted in agricultural systems. Tropical ecologists focused, rightfully in many cases, on natural systems and sequestered themselves in field stations with easy access to undisturbed habitats while the landscape outside of biological reserves and parks was transformed into the pastures, fields, and scrublands with remnant trees that have come to typify the tropics.

Research on the environmental effects of tropical agriculture has blossomed in the past decade. In particular, pages of journals focused on applied ecology, conservation, and sustainable development have been filled with studies that focus on the shaded systems used for growing two major tropical agricultural commodities: coffee and cocoa. This research agenda has been directed first and foremost to the impact that different crop management systems have on local environments, the potential role that diverse shaded cultivation systems have in protecting biodiversity that would otherwise disappear with the loss of natural forest, and the ecosystem services provided by those diverse agroforestry systems.

Along with this, ecologists have used agroforests as model systems to address fundamental questions about tropical ecosystems. Although the heavy human management of plant composition and vegetative structure renders these agricultural systems highly artificial, sometimes this artificial simplicity makes tropical agroforests ideal for exploring basic ecological processes, and these agroforests can be a laboratory for studying phenomena that are difficult to isolate in natural forests.

In this Special Feature, we develop five areas of tropical ecology where research in tropical agroforests has provided fundamental insights into principles governing natural systems: the spatial ecology of multispecies interactions (Perfecto and Vandemeer), the role of epiphytic assemblages in habitat selection of mobile organisms (Cruz-Angón et al.), the role of predators in top-down control of herbivores (Van Bael et al.), the effect of local plant diversity and landscape features on pollinator–plant relationships (Klein et al.), and the relative importance of local habitat features and landscape configurations on functional diversity in insects and birds (Tscharntke et al.). The number of fundamental ecological questions previously addressed in tropical agroforestry systems is far greater than we can cover in these relatively few pages.

Attributes of tropical agroforest systems

Considering the wide range of conceptual areas to which research on managed tropical systems has contributed, we consider it instructive to explore the specific attributes of agroforests that make them useful for ecological studies.

Structural and floristic simplicity.—Agroforest canopies are characterized by reduced structural and floristic (at least in terms of trees and shrubs) diversity. Many agroforests retain the multistrata structure of a tropical forest, but with canopy and understory layers dominated by fewer species. An agroforest shrub layer is comprised of a single crop plant (e.g., cacao and coffee); species that share many life history traits with tropical forest understory plants. A few fast-growing species dominate agroforest canopies. The ecological attributes of the plants in these layers can be explored with greater focus and replicability across individuals than is possible in more diverse systems, a feature that was exploited in the Van Bael et al. study. Furthermore, the reduced diversity of the trees and shrubs can allow for efforts to study other aspects of biodiversity (such as epiphytes, which can be very diverse; see Cruz-Angón et al.). Finally, with fewer species, the functional role and the ecological requirements of individual species becomes more apparent.

Local spatial homogeneity.—The way in which crop and canopy layers of tropical agroforests are planted and managed often results in low levels of spatial heterogeneity at the level of the farm or

[1] Reprints of this 39-page Special Feature are available for $10.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1990 M Street, Suite 700, Washington, D.C., 20036 (esaHQ@esa.org).

collections of adjacent farms. This reduces (not eliminates) the impact of local environmental variability on habitat for mobile organisms that inhabit the farm. These attributes have allowed for empirical testing of ideas of spatial ecology (see Perfecto and Vandemeer), where it is necessary to minimize local environmental effects so that the spatial effect of specific interactions can be detected. In addition, the relatively homogeneous agroforest environment provides ample opportunity for establishing locally repeatable conditions for experiments.

Regional and global homogeneity.—Agroforestry systems are often similar in structure and composition over entire regions and even share a great deal of similarity over large areas of the tropics. For example, coffee grown under an *Inga*-dominated shade can be found throughout the northern Neotropics, providing an opportunity to look at the secondary response of organisms where there are interesting differences in source flora and fauna, climate, and surrounding habitat matrix. The homogeneity of these systems at a broad geographic scale extends to the responding fauna. As argued by Tscharntke et al., insect and bird assemblages in agricultural habitats are characterized by low beta diversity relative to native forest habitats. Regional replicability was a key ingredient in the analysis of the trophic role of insectivorous birds in agroforests (see Van Bael et al.).

Well-defined complexity gradient.—The management systems characteristic of coffee and cacao farms and other agroforest systems can often be arrayed in a well-defined gradient of decreasing structural and floristic complexity, allowing for relatively well-controlled studies of the effects of environmental complexity on specific ecological processes and on biodiversity such as pollinators and the ecosystem service they provide (see Klein et al.).

Well-defined landscape configuration.—Landscape ecology explores the effect of the configuration of habitat features and the local distribution of organisms. Developed areas of the tropics provide landscapes with clearly defined edges and boundaries, reasonably well-replicated habitat units (such as agroforests), and clear distinctions between habitat patches and matrix. These attributes are now being exploited to analyze the role of fragment isolation and spillover effects on functional diversity in tropical landscapes (see Tscharntke et al.). Agroforests often represent the only wooded vegetation in the matrix or along corridors between forest fragments. Their presence and condition provide an opportunity to study the role of habitat quality on immigration and emigration in relict patches of natural vegetation.

Ability to conduct large-scale manipulative experiments.—For clear ethical reasons, it is less problematic to undertake a large-scale habitat manipulation (see Cruz-Angón) in an already managed agroforest than in natural tropical forest, much of which is protected. Such manipulations may serve the dual function of exploring both basic ecological questions and gaining applied information that may benefit the farmer.

What now?

Much of the progress that has been made in basic ecological research in tropical agroecosystems has stemmed from researchers who are already working in the system. Perhaps the time has come to take a more proactive approach, addressing fundamental questions with comparative observations and experimentation in natural and managed systems that are part of an integrated research plan from the onset. A strategic alliance forged on research in the natural and human-managed world allow us to take the fullest advantage of the opportunities that tropical ecosystems provide.

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