VERTICALITY AND HABITAT ANALYSIS: MACARTHUR AND WILSON'S BIOGEOGRAPHY THEORY REVISITED

H. Bruce Rinker

The most striking and important fact for us in regard to the inhabitants of islands, is their affinity to those of the nearest mainland, without being actually the same species.

—Charles Darwin, 1860, On the Origin of Species by Means of Natural Selection

MacArthur and Wilson (1967) proposed "the possibility of a theory of biogeography at the species level" that expressed the relationship between insularity and biodiversity in quantitative terms. They noted that islands constantly gain (immigration) and lose (extinction) species based on their areas and distances to the mainland or other biodiversity sources. Area alone, however, is an insufficient measure of species richness as oceanic islands are very different from "habitat islands," fragments of vegetation in a mosaic of terrestrial environments. Among others, Wu and Vankat (1993) critiqued the theory and debated its validity and its application to oceanic and continental islands as well as to a variety of insular habitats such as city parks and wildlife corridors. Weaknesses in the MacArthur and Wilson theory soon came to our attention. All species cannot be treated the same. Immigration and extinction probabilities are not the same for all species. The theory assumes random distribution of biodiversity in undisturbed habitat while the sustained occurrence of a particular species may necessitate the presence (or absence) of other types of organisms. All areas of island habitats are not equally accessible or preferable for species' colonization.

Generally speaking, the MacArthur-Wilson equation is inadequate because it is two-dimensional and does not clearly address the widely recognized multidimensional aspects of landscape structure and what Janzen calls "the eternal external threat" (1986): the external nonhuman and unintentional human threats to island preserves. Today, a more accurate approach to the tough complexities of living (as opposed to theoretical) islands is that of Forman's Land Moses (1993). Studies on dendrobatid frogs and their reliance on canopy bromeliad tanks, for instance, or on euglossine bees and their complex interdependencies on orchids and Brazil nut trees illustrate the formula's inadequacies. Like fractals, all the co-variables governing species richness may approach infinity, depending on spatial-temporal scales.

Canopy ecology presented two related shifts in biogeography perspective apropos to this discussion:

- The term *canopy* is now defined as the combination of all leaves, twigs, and small branches in a stand of vegetation (Parker 1995). Indeed, to be even more expansive, a forest canopy is all aboveground vegetation including the crowns and trunks of its trees, its biota, and its ecological processes. The meaning of canopy may be expanded eventually to include the entire column of life sandwiched between atmosphere and bedrock including soil biodiversity!

- The term *canopy* emphasizes the verticality in a stand of vegetation. No matter which spatial-temporal scales are applied to forest habitat analysis, a complex stratification of biota exists that is ignored by a strict interpretation of the MacArthur-Wilson formula. Area is a simple two-dimensional measure, but organisms live in a sometimes baffling complexity of four dimensions: space plus change through time.

Continued
VERTICALITY AND HABITAT ANALYSIS: MACARTHUR AND WILSON'S BIOGEOGRAPHY THEORY REVISITED—cont'd

Organisms are found across a four-dimensional landscape. In the past decade, canopy work with mammals (e.g., Malcolm 1995), neotropical migrants (e.g., Rinker 2001), and arthropods (e.g., Stork et al. 1997) have confirmed that reducing biological complexities to a species-area curve is an inadequate reflection of the natural world. With the emergence of canopy ecology, the dynamic vertical aspects of habitats (e.g., architecture and light penetration in aging forests) provide a richer detail about the distribution of biota.

Ecosystems may no longer be treated as predictable machines with scientific theories as crisp, explanatory models for organisms. They cannot be approached as small-number assemblages (i.e., individuals in a collection) or as large-number means (i.e., averages in a collection). Neither extreme adequately describes the system. Living systems are stochastic, uncertain, and somewhat chaotic; their coupled generalizations cannot be ossified into species-area regressions. Systems are too difficult to grasp by word or formula so their theories are really signposts to what really is. They point the way to more research, more study, and more experimentation; but they are never enough in themselves.

When MacArthur and Wilson wrote The Theory of Island Biogeography in 1967, canopy ecology had not yet emerged as a formal discipline with established protocols and firm definitions. Canopy ecologists have since learned that forests are messy systems profiled like a cerebral cortex and that verticality is one of a number of features important for the distribution of ecosystem biota. Canopy ecology has disclosed the mythological aspects of the MacArthur-Wilson formula: it is only a stepping-stone toward a better understanding of ecosystem complexity.

References


Another issue that relates forest canopy research to forest management concerns the effects of forest fragmentation on forests and their associated canopy biota. Some canopy researchers have shifted their research locales away from primary forests in order to examine questions posed by trees growing in secondary forests or those isolated in pastures or other agricultural settings. They have begun to address the question of whether a few trees or even a single tree crown can function in a pasture or clear-cuts in terms of the biota it might support. Can pollinator and disperser animals cross open spaces? Can epiphytes found in old-growth trees disperse and maintain themselves, or will the epiphytes ultimately be only those that can survive under edge conditions?
Forest Canopies

Second Edition

Edited by

Margaret D. Lowman
Professor of Environmental Studies
New College of Florida;
TREE Foundation
Sarasota, Florida

H. Bruce Rinker
Center for Canopy Ecology
Marie Selby Botanical Gardens;
TREE Foundation
Sarasota, Florida

ELSEVIER
ACADEMIC PRESS
Amsterdam • Boston • Heidelberg • London
New York • Oxford • Paris • San Diego
San Francisco • Singapore • Sydney • Tokyo