
Colonizing Plants: Evolutionary and Ecological Trade-offs

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The first publication that most significantly influenced my ecological thought was not a single paper. It was a book, *The Genetics of Colonizing Species* (TGCS) published in 1965 and edited by H. G. Baker and G. L. Stebbins. This 588-page book comprises 25 research papers and discussions from the first symposium sponsored by the International Union of Biological Sciences held in 1964.

The five-day symposium brought together ecologists, taxonomists, and geneticists to summarize knowledge about colonizing species and to exchange ideas about the kinds of evolutionary changes that occur when organisms are introduced into new territories. Twenty-seven authors from nine countries produced 25 outstanding papers; those that influenced me most were papers by R. W. Allard, H. G. Baker, L. C. Birch, T. Dobzhansky, F. Ehrendorfer, J. L. Harper, C. B. Heiser, R. Lewontin, E. Mayr, G. A. Mulligan, K-I. Sakai, G. L. Stebbins, C. H. Waddington, and E. O. Wilson. The discussions at the end of each chapter were distinguished by extensive and lively exchanges of facts, the latest thinking, and unresolved questions open to future research.

A sense of adventure and excitement leapt off the pages when I read the book in 1968. For example, in the summary chapter, Ernst Mayr wrote, “Natural selection always achieves only a compromise, all fitness is a compromise, and gaining an advantage in one way usually means abandoning some other properties.” What a concept to stimulate the imagination of a budding ecologist: evolutionary/genetic trade-offs that had ecological causes and consequences! I was finishing a Master’s degree in Plant Systematics with Prof. John Beaman, and entering a Ph.D. program in Plant Ecology with Prof. John Cantlon, both at Michigan State University (MSU). With this switch in subject matter and major professors, I was moving from an emphasis on evolutionary botany to my growing interest in the ecology of plants in disturbed or successional systems.

About this same time, I also discovered and gained inspiration from a classic paper by Clausen, Keck, and Hiesey (Clausen et al. 1940) where morphological phenotypes (several subspecies) of the herbaceous plant *Potentilla glandulosa* were taken from populations naturally growing in overlapping ranges across an altitudinal gradient in California and then transplanted into common gardens at three different elevations. The researchers examined two major questions: the contribution of genetic differences and phenotypic plasticity to variation in morphology, and the interactions between plant variation and environment, which in turn explained the differences in distributions across the gradient by various subspecies. The combination of evolutionary/genetic and ecological questions was particularly appealing.

Another publication that was influential to my early development was *The Theory of Island Biogeography* (TTIB) by R. MacArthur and E. O. Wilson (1967). This book provided one of the theoretical bases for some of my empirical research on dispersal and establishment, local extinctions,

succession, and community diversity, and also complemented the experimental field approach taken by MSU researchers.

Indeed, my first (1977) publication in *Ecology* (58:840-849) opens with this paragraph: “With few exceptions, each plant species is a colonizer at some time. Individuals invade an area already occupied by other more-or-less cohesive plant associations and garner enough resources from the site to produce propagules (the only means of movement to yet another site) before dying. The species eventually becomes locally extinct.” The ideas, if not the exact references, in TGCS and TTIB had clearly influenced my thinking.

The concepts, questions, and field-experimental approach addressed in TGCS, CKH, and TTIB are evident in many of my other research publications and those of the graduate students and post-doctoral fellows who worked with me at MSU in the 1970s and 1980s: cf. J. D. Soule, K. L. Gross, A. L. Harbeck, R. S. Gross, D. E. Goldberg, M. A. Potvin, J. S. Harrison, C. R. Cid-Benevento, T. E. Miller, A. A. Winn, C. L. Jolls, and B. Pors.

The paper trail is long and with many branches, but I will not attempt to give details in this short communication. Suffice it to say that the concepts and approaches to questions raised in TGCS, CKH, and TTIB extend to include research at the level of Individual Plant Species (e.g., adaptive significance of various physiological and morphological traits, reproductive effort, seed dormancy vs. dispersal or seed number vs. seed size trade-offs), Species Interactions (e.g., competition and co-existence; diffuse competition; functional groups), and/or Communities and Landscapes (diversity vs. productivity, niche overlap across gradients of space and time, succession patterns and processes). In general, the field research used experimental methods and hypothesis testing. Most papers focus on the responses of plants to environment, whereas others focus on the effect of environment on plants—we always understood that these two foci are not equivalent, but instead, complementary, yielding greater insights into plants and plant communities than is possible by a single approach (e.g., Miller and Werner 1987).

In the 1990s, my research turned to questions of tree population dynamics and community structure in the highly dynamic savannas of northern Australia. The ideas inspired by the early publications cited above, and enhanced by countless other key papers over the previous two decades, continued to inform my research, and do so today. For example, my most recent publication (2013), in *Ecological Monographs* (83:67–93), addressing the strong demographic bottlenecks to the transition of persistent juvenile trees to the canopy layer, uses a field experimental approach that links tree morphological, physiological, and phenological attributes (all of which vary with size and life history stages) to the growth and demographic responses to competition and disturbance, and ultimately to landscape-scale variables. In effect, it is the colonization phase of the life history of the canopy tree species that determines the physiognomy of these savannas. The paper is yet one more step on the paper trail from CKH, TGCS, and TTIB.

Today, the TGCS book would be likely be entitled “Evolutionary Biology of Colonizing Species.” Even though modern genetics and its techniques were not available 50 years ago, the concepts, ideas, and questions inherent in this book’s chapters continue to be relevant to ecological and evolutionary thought today.



Fig. 1. Pat Werner leaning on buffalo fence, Kapalga.



Fig. 2. Pat and longnecked turtle, 1987.

Literature cited

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