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Making Sense of Ecological Complexity: A Personal and Conceptual Retrospective

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ABSTRACT

The Organization for Tropical Studies (OTS/OET) played an important role in the development of population and community biology during the first 25 years of the organization's existence. The author traces changes in the conceptual framework of community ecology during this period, using examples from his own work with hummingbird flower mites and from the tropical research of others who have been associated with OTS. The principal lesson to be learned from this period is that the same pattern may result from several different processes; there are distinct, valid explanations for different cases of what tropical ecologists used to see as a unitary phenomena.

RESUMEN

La Organización para Estudios Tropicales (OET/OTS) ha jugado un papel importante en el desarrollo de la biología de poblaciones y de comunidades naturales durante sus primeros 25 años. El autor indica cambios en la estructura conceptual de la ecología de comunidades en estos años, con ejemplos tomados de su propio trabajo con ácaros florales de colibríes y con investigaciones de otros biólogos asociados con la OET. La lección principal que esta epoca nos deja es que el mismo patrón puede resultar de distintos procesos. Hay explaciónes válidas para diversos casos que los ecólogos tropicales veían anteriormente como un fenómeno unitario.

Key words: *community ecology; hummingbird; mite; Organization for Tropical Studies; theory.*

IN A FIT OF RETROSPECTION, while trying to assess the role of the Organization for Tropical Studies (OTS) in 25 years of tropical population biology for a 25-minute talk, I found myself wondering how I ever got involved in tropical biology in the first place. So I will begin with a brief, personal preface, which I suspect parallels the stories of scores of other biologists whose lives and careers have been shaped by OTS—though the details, of course, will differ.

As a Colorado ranch boy who had somehow endured three years with the sherry set as an English major at Harvard, I was an easy mark for biology in my senior year, when I took E. O. Wilson's course in population biology (Wilson & Bossert 1971). I finished that course in the same year that OTS was taking form. Somehow, among the many other topics in the course, species interactions and patterns of species diversity were the subjects I found most intriguing.

After graduation, I worked for eight months for Richard Schultes in the ethnobotany museum at Harvard, accessioning and organizing strange and wonderful plant products from the tropics—not all of them legal these days (Schultes 1963). Schultes

was full of tales of ethnobotanical discoveries and pharmacological experiences during his years among the indigenous peoples of the Amazon and the Orinoco (Schultes 1988). His heroes were Charles Dickens (especially *Pickwick Papers*) and Richard Spruce (1908), both of whom I read as part of my duties in the Museum. My interest in tropical biology grew stronger.

My first year in graduate school at the University of Michigan I was assigned to a space in Marston Bates' laboratory. Marston was such a tropicophile that he had developed a sizable part of his Ann Arbor home into a miniature tropical forest, complete with plants, nesting birds, lizards, and insects (Bates 1970). He used to tell us stories of life in the Colombian Amazon, where he had lived and worked for more than a decade on yellow fever research (Bates 1949). Marston hated winter (Bates 1952). In fact he claimed that, when he first moved to Ann Arbor to take a faculty position, he had driven around checking those lighted time-and-temperature signs you see on banks, looking for the warmest place to keep his money. When I asked him once for his own explanation of the richness of

tropical biotas, Marston provided a very simple explanation: "Wouldn't YOU rather live there?"

In the summer of 1966, then, in my first year of graduate school at the University of Michigan, I jumped at the chance to take an OTS field course in Costa Rica, in the mysterious tropics. By then I had read everything I could find on patterns of species diversity, from Henry Walter Bates (1864) and Alfred Russel Wallace (1869, 1878, 1889) to Robert MacArthur (1960, 1965; Klopfer & MacArthur 1960, 1961). I was ready to head up some dark, canopied river in a dugout canoe, delightfully overwhelmed by the sounds and colors and smells of "biotic diversity." And I did get that canoe trip, from Puerto Viejo to Finca La Selva—before bridges and before roads. But, like the course, it was far too short.

Soon, several of us from that course were back in Costa Rica, for teaching and for research—among them Gilbert (1971, 1972), Arnold (1972), Futuyma (1973), and Jeanne (1975). My OTS independent research project with niche breadth and diversity of insects on rotting bananas turned into a dissertation (Colwell 1969, Colwell & Futuyma 1971). Later, a field problem from OTS course 69-1, which I taught with Norman Scott and Arthur Weston, turned up the hummingbird flower mites that have been the mainstay of my field research and the inspiration for my theoretical work ever since (Colwell 1973, 1985a, 1986a, b; Heyneman et al. 1991).

CHANGING VIEWPOINTS IN TROPICAL POPULATION AND COMMUNITY BIOLOGY

Looking back at tropical research in population and organismal biology over those 25 years as a sort of "conceptual river," we can see the silting-up of some older channels as new ones capture the flow. Some meanders have been left aside as oxbow lakes, others have filled up and been forgotten. New side streams have developed from unexpected sources, and seeming backwaters have sometimes begun to move again. One thing is clear: the flow of ideas and research has increased enormously in volume, thanks in great part to OTS. And as a result, the rivercourse has become increasingly complex and dissected, promoting a healthy degree of differentiation and local adaptation.

I will try to trace some of these changing patterns of concepts and research, focusing primarily on questions of community structure and biodiversity. I will cite an idiosyncratic selection of papers,

focusing, where possible, on authors who have benefited from OTS courses or research facilities—with apologies to all whom I have neglected in my ignorance. I will shamelessly insert a few examples from my work with the mites, to add something concrete.

SPECIES INTERACTIONS.—In the mid-1960s, when OTS was born, we saw biological communities as tightly integrated wholes, tied together by balanced conflicts among the component species. Within trophic levels, the conflict was competition for resources (e.g., MacArthur & Levins 1967, Levins 1968). Between trophic levels, the conflict was between the consumers and the consumed—predators and prey (Holling 1959, Rosenzweig & MacArthur 1963); few ecologists studied parasites in those days, though we sometimes remembered to mention them.

Mutualism, which is in fact another kind of balanced conflict, was largely treated as a curiosity and not seen as a conflict at all. Soon, however, intensive studies of the reproductive biology and pollination of tropical plants (e.g., Baker 1970, Frankie et al. 1974) and of pollinator assemblages (e.g., Colwell 1973, Stiles 1975, Feinsinger 1976, Wolf et al. 1976) in Costa Rica began to direct our attention to the key subject of mutualistic relationships on a community level. Other researchers in Costa Rica carried out pioneering studies of the role of insects and vertebrates in fruit and seed dispersal in tropical habitats (e.g., Janzen 1971, Fleming 1979). Janzen's work with the ant-acacia system (Janzen 1966), which Thomas Belt (1874) first described, stimulated hundreds of students to explore the ecology and evolution of tropical mutualisms. Today, the study of mutualisms is among the most important areas in tropical biology (Boucher 1982). Moreover, I suspect that a careful historical study might reveal that the enthusiasm generated by tropical studies has been responsible for propelling the increasing interest in the evolutionary ecology of mutualisms in temperate latitudes.

STABILITY AND COMPLEXITY.—In the late 1960s, the hottest hypothesis of the day was that biotic diversity begets community stability, whatever that might be (MacArthur 1955, Woodwell & Smith 1969). In the early 1970s, while others attacked the foundations of this principle on theoretical grounds (May 1973, Goodman 1975), Futuyma published a key paper (which grew out of discussions in an OTS course) arguing almost the reverse (Futuyma 1973). Making explicit what many tropical biologists had come to suspect by then, Futuyma suggested that

the high biotic diversity of tropical communities, rather than producing stability, is permitted by the high degree of predictability and relatively low amplitude of variation in climatic factors in the tropics. In fact, he claimed, diverse communities in the tropics may not be as resilient to external perturbation as simpler communities elsewhere.

Although this idea now appears oversimplified, it crystallized a deeply changed point of view for many of us, and helped to stimulate research while kindling a new urgency in our commitment to conserving tropical habitats. In the following decade, great progress was made, much of it at La Selva or by OTS graduates elsewhere, in comprehending the dynamics of tropical forests and the limits of their actual resilience (e.g., Hartshorn 1978), and this work continues (see Denslow 1987).

EVOLUTION AND COEVOLUTION.—In the 1960s, although evolution was of course regarded with appropriate reverence as the source of adaptation, we ecologists believed that "evolutionary time" and "ecological time" were distinct by at least a few orders of magnitude (Wilson 1969), although Hutchinson (1965) foreshadowed a more interactive view. Many believed that contemporaneous evolutionary change could be safely ignored in the ecological study of demographic and geographic patterns.

Over the past 25 years several developments in evolutionary biology have challenged this view. The idea of coevolution, in large part first stimulated by the classic paper by Ehrlich and Raven (1964), has become an increasingly important part of our thinking about communities (Futuyma & Slatkin 1983). Using field and laboratory experiments and the tools of quantitative genetics, studies of adaptive response to selection based on species interactions have begun to reveal a surprising potential for rapid evolutionary change (e.g., Reznick et al. 1990). Research on the genetic structure of populations and levels of genetic diversity within them has made it clear that evolutionary and ecological time are often commensurate. Meanwhile, the rapid, widespread evolution of biocide resistance in bacteria, fungi, plants, insects, and even fishes and mammals points out the potential for rapid adaptive change in response to anthropogenic environmental change.

The origin and rapid growth of the field we have begun to call evolutionary ecology (Colwell 1985) owes much to the efforts of tropical biologists, in part, I suspect, because both ecological and evolutionary processes tend to proceed more rapidly in the tropics. Just as ecologists have begun to study the role of genetic variation and selection in their work, evolutionary biologists increasingly carry out their experimental work in the "ecological theater" (Hutchinson 1965).

TAXONOMIC SCOPE.—In the years when OTS was young, active areas of ecological research were even more biased taxonomically than they are today. Studies of the organismal and population ecology of tropical plants—an active field today (e.g., Chazdon 1986, Clark & Clark 1988, Dirzo et al. 1988)—seemed virtually nonexistent before 1970. Small, ugly, and/or brown arthropods were generally disdained, and still are, unless they happen to be social. As far as I know, my collaborators and I are still the only biologists working on the natural history and evolution of noneconomic, free-living tropical mites, even though there are probably more than a half a million species of them—nearly all undescribed.

COMPETITION, RESOURCE PARTITIONING, AND PATTERNS OF SPECIES DIVERSITY.—Hummingbird flower mites (Rhinoseius and some species of Proctolaelaps, Ascidae: Gamasida) breed and feed on nectar and pollen in the flowers of hummingbird-pollinated plants. They move on foot between successive flowers in the same inflorescence, but they mount the bills of visiting hummingbirds to travel among inflorescences and plants (Colwell 1985b). We now know that hummingbird flower mites are found from California to Chile, but are most diverse in the lowland wet tropics (Colwell 1979, Colwell & Naeem 1979). A closer look at the conceptual history of our work with these mites mirrors several important shifts in the study of communities in general, especially tropical communities.

Because nearly everyone believed in the 1960s that resources were partitioned competitively, we expected to find clear, strong ecological distinctions among coexisting species. The first ecological study of hummingbird flower mites, which I carried out in 1971 at Cerro de la Muerte in Costa Rica (Colwell 1973), made me a believer in this orthodox view. The two resident species of hummingbird flower mites in this high elevation (3100 m) community, later described as Rhinoseius colwelli and R. richardsoni (Hunter 1972), each monopolized a completely different set of host plant species, with no overlap whatsoever, yet both could be found together on the same hummingbird. "Transplant" experiments showed that each mite species could survive and reproduce when on its own in virgin flowers of a host normally inhabited by the other species; ex-

ploitation competition seemed unlikely, in itself, to explain the neat partitioning of resources. When placed together in arenas (Petri dishes), however, the two mite species engaged in mighty battles to the death—males of each species attacking and sometimes killing both sexes of the other species.

In this case, interference competition certainly seemed to account for the complete lack of host-sharing in nature, and would clearly select for accurate host-finding behavior. Too often in those days, though, when we found strong distinctions in resource use, we were inclined to conclude that competition must be responsible for them, without any direct test at all. Thinking that the prejudices of the times might have misled me, I tried this experiment again in 1982, with the same outcome, and in fact it has been repeated by generations of OTS students.

In the intervening years, the burden of proof has been transferred squarely to the shoulders of anyone claiming a role for competition, whether in the intraspecific form we call density dependence, or in the interspecific forms we distinguish as exploitation competition and interference competition (or the equivalent phenomena in botanical terminology). One of the first and most influential challenges to the orthodoxy of competitive structuring of guilds came from the work of Strong (1982) at La Selva and elsewhere in Costa Rica, with the hispine beetles that live in the rolled leaves of Heliconia. Not only was Strong unable to demonstrate any role of competition, there was virtually no resource partitioning, in sharp contrast with hummingbird flower mites.

Meanwhile my collaborators (Shahid Naeem, David Dobkin, and Amy Heyneman) had moved on to lowland assemblages of hummingbird flower mites. (Somewhere around 1980 we began to try to remember to say "assemblage," a term with fewer presumptions and less historical baggage than "community".) We first worked in the Arima Valley in Trinidad and later at La Selva in Costa Rica. For the Trinidad system, we have a virtually complete picture of the distribution of mites among host plant species and among hummingbirds. At least 16 species of hummingbird flower mites coexist there, each monopolizing a single host plant species or a specific, sequentially flowering set of species. As in the simpler system at Cerro de la Muerte in Costa Rica, the occurrence of each species of mite in Trinidad is rigidly restricted to its usual host plant repertoire, yet they are often mixed on their hummingbird carriers. We have now learned that substances found in nectar are cues for disembarkation (Heyneman et al. 1991).

It is apparent from this pattern and from the phenology of the host plants that every physiologically suitable potential host species that flowers all year round supports at least one monophagous species of hummingbird flower mite. In contrast, where flowering periods are seasonal, especially at high elevations (Colwell 1973) or high latitudes (Colwell & Naeem 1979), mite species must become "sequential specialists" on successively flowering host species. Additional studies at Monteverde, Costa Rica; in Mexico; in California; and in Chile provide further evidence for the same pattern (Colwell 1986a). These patterns are so consistent among communities that, before we began work on the mites at La Selva, we were able to predict quite accurately the number of hummingbird flower mite species that the Heliconia flora of La Selva supports simply by analyzing the phenology records for the plants that Stiles (1978) had published.

The conjecture that more constant resources promote greater biotic diversity through more precise resource partitioning (Klopfer & MacArthur 1960, MacArthur 1969) is certainly confirmed for hummingbird flower mites (although the orthodox mechanism, interspecific competition, is probably not responsible, as discussed below). In contrast, the few herbivorous insect groups that have been closely studied on a latitudinal transect apparently fail to show this pattern (Price 1991); most are highly specialized at all latitudes.

In fact, the more closely ecologists have looked at patterns of diversity, the more clearly we have established the inadequacy of single-factor explanations for latitudinal gradients in species diversity. The role of regional biogeography and historical contingencies (Ricklefs 1989), patterns of disturbance (Huston 1979) and immigration (Stevens 1989) in relation to competitive exclusion or extinction, and fundamental aspects of climate (Currie 1991) are all clearly involved.

NONCOMPETITIVE CAUSES OF RESOURCE PARTITIONING.—Meanwhile, back in Trinidad, once we had worked out the patterns of host affiliation and hummingbird carrier usage, we set about to look for evidence of interspecific competition among the hummingbird flower mite species there. Expecting carnage when we put species together in arenas, as I had found at Cerro de la Muerte, we found instead (depending on the species pair) either no interaction at all, or interspecific attempts at courtship, or aggressive interactions, but only ritualized charges and retreats, no real damage.

Not only is interference (aggressive) competition

quite unlikely to account for the rigid resource partitioning of host plant species by hummingbird flower mites in Trinidad, but we have tried and failed to find any evidence for exploitation competition either, and in fact have produced considerable evidence against any major role for it (Colwell 1986a). To make matters even worse for the orthodox view of competitive resource partitioning, we soon found cases of entirely coincident niches. Flowers of the plant *Cephaelis muscosa* (Rubiaceae), for example, consistently support two hummingbird flower mite species, *Proctolaelaps contumex* and *Rhinoseius hirsutus,* neither found on any other host plant. Not only is there no aggression between these species in arenas, but they are positively correlated in incidence among inflorescences, and positively correlated in abundance among occupied inflorescences. The same pattern is repeated for host-sharing species in *Heliconia bihai* (Heliconiaceae) in Trinidad, in *H. tortuosa* at Monteverde, Costa Rica, and in *H. imbricata* at La Selva (Colwell 1986a), with different mite species, but in each case a *Proctolaelaps* species and a *Rhinoseius* species share the same host.

Selection for survival and potential fecundity, however, is not the only cause of adaptive evolution. Sexual selection, which arises from differential mating success of different genotypes (Arnold 1983), is a powerful force that has not previously been given much importance in studies of resource partitioning. Hummingbird flower mites live in their food, the supply of which often appears to exceed the demand in the flowers they inhabit. Especially when food is not in short supply, mate finding may be just as important a focus of selection as food-finding. I have proposed that, for these mites, fidelity to a particular host species may maximize mating success—an idea I call the "host fidelity hypothesis" (see Colwell 1986a for details and for a historical review of this idea). In other words, for a mite, the best place to find an appropriate mate is in the usual host plant of that mite species. A simple model demonstrates that selection will tend to narrow host repertoires to the narrowest, phenologically possible set, under selection for mating success alone (Colwell 1986b)—a form of sexual selection.

The fact that when two mite species do share a host species, they are (so far) invariably members of different genera only strengthens the case for this hypothesis. It seems reasonable that two mite species can use the *same* host species as a place of sexual rendezvous if courtship and morphology differ enough to prevent mistaken matings, which seem more likely to occur between members of the same

genus than between noncongeners. Other systems in which sexual selection for host fidelity is implicated include the true fruit flies (Tephritidae) (Prokopy *et al.* 1982), certain tropical grasshoppers (Rowell 1978), and a group of beetles that inhabit the heads of thistles (Zwölfer 1974), but few ecologists have been looking at the effect of mating behavior on ecological distributions, so the phenomenon may be more widespread.

But sexual selection is only one of several noncompetitive mechanisms implicated in producing nonrandom resource partitioning or nonrandom morphological distinctness within guilds (Futuyma 1983). Gilbert (1975), for example, has argued that the leaves of co-occurring *Passiflora* species have diverged in form as a frequency-dependent escape from oviposition and herbivory by *Heliconius* butterflies. At the next trophic level, it now appears that herbivores may sometimes be monophagous principally because they escape their own predators best on particular host plants. If the predator is frequency-dependent in its feeding, we might expect nonrandom dispersion of herbivore species among physiologically acceptable host plants (Bernays & Graham 1988). Finally, believe it or not, some resource partitioning in some kinds of organisms is doubtless caused by genuine interspecific competition. Hummingbirds are probably an excellent example (Wolf *et al.* 1976, Feinsinger & Colwell 1978).

CONCLUSION

This allegorical account points out what I see as the primary lesson from tropical population and community biology during the past 25 years. Tropical population and community ecologists have become better organismal biologists and better natural historians. We have come to realize that, while broad patterns may still be found and should still be sought, the particulars of the daily lives of real organisms and the scale and patterning of their environments matter profoundly, creating a rich diversity at the level of process. The important point is that there are clearly distinct, valid explanations for different cases of what we used to see as a unitary phenomena. It would be stretching things to insist that most of the changes would not have taken place without OTS. But there is no doubt in my mind that the unique OTS mix of hands-on education and research facilitation, of nurturing and networking have left a bold signature on the history of population and community ecology.

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