THE STATE OF THE ART IN COMMUNITY ECOLOGY

ERIC R. PIANKA*

CONTENTS

Abstract: Many major advances have been made at various levels in biology, but the approach at the community level has stalled. Community ecology remains in its infancy and lags far behind other organismal and suborganismal disciplines due to its innate complexity, multi-dimensionality, multiple causality, as well as the extensive scale in space and time involved and serious empirical difficulties of data collection and analysis. Pristine natural systems are vanishing rapidly before we have learned how they are organized or how they behave. The study of communities must of necessity remain to some degree abstract and complex. Community ecology is also extremely promising and important, as well as exceedingly urgent. Major new insights could well lie just around the corner. Community ecology is not for the faint at heart, however; it is one of the most challenging and most difficult of all sciences. We are still in the process of developing a vocabulary. Identification of appropriate aggregate variables or *macrodescriptors* is not only essential, but also constitutes a double-edged sword: macrodescriptors enable progress but simultaneously constrain the discipline's directions. At this early stage in community ecology, it is perhaps safest not to become overly "locked in" by words, concepts, and methodologies. A diversity of approaches seems desirable.

Many community-level properties are probably simply epiphenomena that arise from pooling component populations; examples would presumably include trophic levels, guilds, subwebs, and ecological pyramids. Do communities, however, also possess truly emergent properties that transcend those of mere collections of populations? For example, are patterns of resource utilization among coexisting species co-adjusted so that they mesh in a meaningful way? If so, truly emergent community-level properties arise as a result of orderly interactions among component populations. This fundamental question needs to be answered. Either way, transcendent phenomena or epiphenomena cannot be studied at the level of individuals or populations, but at the level of community ecology.

A major pitfall for community ecologists is that communities are not designed directly by natural selection (as are individual organisms). We must keep clearly in mind that natural selection operates by differential reproductive success of individual organisms. It is tempting, but dangerously misleading, to view ecosystems as "superorganisms" that have been "designed" for efficient and orderly function. Antagonistic interactions at the level of individuals and populations (such as competition, predation, parasitism, and even mutualisms) must frequently impair certain aspects of ecosystem performance while enhancing other properties.

The traditional ecological approach to population interactions has been to consider species in pairs. While fruitful, this focus has diverted atten-

* Department of Zoology, University of Texas, Austin, Texas 78712, USA.

tion away from a more holistic systems-level approach. We must now make a determined effort to understand indirect as well as direct interactions within complex networks of interacting species. Properties of such networks themselves need to be evaluated. Approaches that incorporate mutualism and variable intensity in interactions must be developed. Competitive interactions should also be included and distinguished from the vertical ones that operate between trophic levels. Strong interactions may be more important than weak ones, but the cumulative effects of many weak interactions (as in diffuse competition and diffuse coevolution) could nevertheless be considerable. We need to ascertain the extent to which indirect effects can and actually do balance direct effects.

Whereas the reductionistic approach has been quite successful in other scientific disciplines, it will not lead to generalizations in community ecology. A holistic approach is required. In this chapter, I present examples from my own research. A hybrid protocol for the analysis of community structure has been developed that incorporates resource availability, electivities, nearness rank of neighbors in niche space, null models, and Monte Carlo statistical methodology. This new approach facilitates graphical comparisons of very different systems and is illustrated using assemblages of neotropical fish plus Australian and Kalahari desert lizards.

Another neglected area with promise in community ecology is the effect of large-scale regional factors on the diversity and community structure at the local level. Most ecologists, including myself, have focused on local-level processes. To illustrate the regional approach, I briefly describe some of my own work in progress on the fire succession cycle in inland Western Australia.

INTRODUCTION

I SAW MY FIRST LIZARD ON A TRIP MY PARENTS made across country when I was about six years old. I still remember it, an *Anolis* at a roadside park. I recall doing my utmost to capture this lizard and breaking its tail off, but not being able to catch it. About a year later I caught my first snake, a *Thamnophis*, which soon escaped. Then, in the second grade, I discovered that the classroom next door had a baby alligator. I was transfixed by that alligator and stood by its aquarium for hours on end reveling in its every move. I suspect that most herpetologists had similar experiences in their childhood. This fascination with and commitment to the animals is what binds us and our discipline together.

In short, I knew I was destined to become a biologist even before I had any real inkling of what science was. In graduate school, I discovered the layers in the biological cake (Figure 1), and eventually I became an ecologist.

LEVELS OF APPROACH IN BIOLOGY

Recently, a group that consisted of David Hillis, Michael Ryan, Rafael de Sá, and myself, jointly taught a course in herpetology at the University of Texas. This was an illuminating experience for me. What made it salient was that most courses in the traditional academic situation specialize in the layers—and I was really struck with the wide range of subjects included in our herpetology class. We covered all the levels of approach, from molecules through organisms and populations to communities. The remarkable thing about meetings like the First World Congress of Herpetology is that such a broad spectrum of levels of approach is represented. Herpetology,

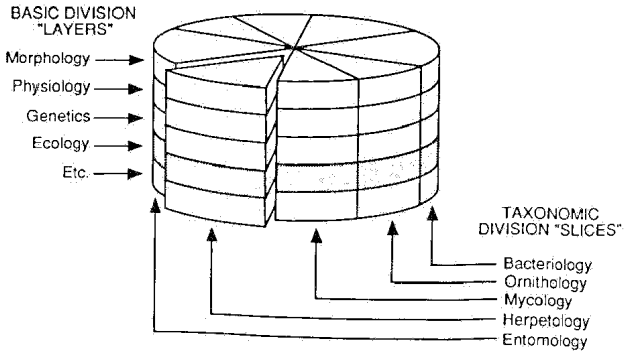


FIGURE 1. The disciplines of biology can be represented as a layered cake, with functional layers (horizontal) and taxonomic slices (vertical). Herpetology has a greater depth than ecology, which has greater taxonomic breadth.

like biology, is a vast subject. One of the things that makes the herpetological approach so fruitful is that it generates interdisciplinary research and promotes tolerance and appreciation across the various levels of approach. Workers at different levels too often look somewhat askance at the next higher level of approach: molecular biologists are slightly suspicious of cell biologists; cell biologists are just a little wary of physiologists; physiologists are a bit suspicious of behaviorists and other whole-organism biologists; and on it goes. Unfortunately, many population ecologists distrust community ecology. The reason for this hesitancy to accept the next higher level may be that one must slur over interesting detail at one's own level in order to practice biology at the next higher level.

Ecologists are not very interested in captive animals. As far as ecologists are concerned, the California condor is already effectively extinct. Our subjects are wild organisms in natural settings—a (hopefully) pristine natural environment to which that organism has become adapted and in which it has evolved. Rolston (1985) made a useful analogy: he likened life on earth to a book written in a language that humans can barely read. Biologists are just now acquiring the skills necessary to read and decipher this book, but the poor book is tattered and torn, pages are missing (which represents extinct species such as passenger pigeons), and some chapters have been almost entirely ripped out (like the tall grass prairies of midwestern North America). There is a considerable urgency to study wild organisms in pristine natural habitats now before they are gone forever.

As we look at different levels of approach, we encounter vast differences in space and time scales (Figure 2). Molecular biologists can do experiments in test tubes or in small spaces in rooms in a matter of days or weeks. Sometimes it is actually possible to plan a critical experiment before lunch, execute it that afternoon, and analyze the results that evening or the next day. As one ascends to higher and higher levels, larger areas are required and more time is needed (Schoener 1989; Menge and Farrell 1989). Cell and molecular biologists study entities that are much smaller than themselves and they therefore rely on powerful enlargements to examine their systems, whereas community ecologists study systems that are much larger than themselves and hence they require equally powerful reductions to perceive their subjects. Thus, for community ecologists, the analogue of electron micrographs is macrographs, or satellite images (see the last section of this chapter). Community ecology requires thousands of square kilometers and decades or even centuries, making it an imposing subject. I would like to take this opportunity to make a provocative and "idiosyncratic" statement about the current state of the art of community ecology, drawing examples from my own work.

The scientific method has virtually become equated with the reductionistic approach. As scientists, we are all trained first to break up what we are studying into its component parts and then to try to understand how those parts and components interact with one another.

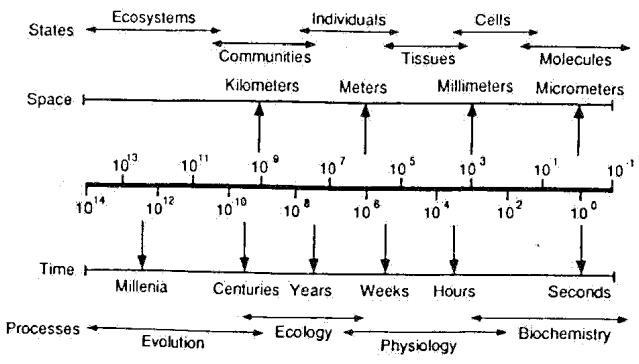


FIGURE 2. Diagrammatic representation of the time and space scaling of various biological phenomena. Community and ecosystem phenomena occur over longer time spans and vaster areas than organismal- and suborganismal-level processes and entities.

This very fruitful approach has led to many important discoveries. For example, at the lowest level in biology are all the elegant biochemical findings, such as the discovery of DNA and RNA, which are the machinery of genetics, transcription, translation, and so on. As one ascends the hierarchy of biology, equivalent discoveries have been made in cell biology and physiology. At the level of the whole organism, we encounter the concept of natural selection and important ideas about adaptive components of behavior. Even at the population level, a discovery of considerable importance has been made, namely the notion of kin selection. At the community level, however, we remain abysmally ignorant. We cannot afford to allow community ecology to languish any longer. It has fallen well behind the other types of biology and we need to try to catch up.

Why has community ecology remained so primitive? Obviously it is not for the impatient or timid. Not only is it not easy, but it requires a long time and a lot of space. Results do not come in overnight. Community ecology also demands considerable theoretical prowess because it is very abstract, conceptually difficult, and multi-dimensional. It is empirically intractable, too. A lot of devotion and hard work are necessary to collect any kind of data on an entire system or even a portion of one. There are serious empirical problems of data collection and analysis. Multiple causality may well be more of a problem in community ecology than it is at lower levels because its time and space scales are so vast. Many biologists, including population ecologists, find community ecology repugnant, and they shy away from it, for understandable reasons.

Ironically, population ecologists are some of the worst foes of community ecology. Community ecology has to attract population ecologists who are well versed in natural selection. Our discipline has become the province of systems ecologists and ecosystem engineers—we need more "born-again" population ecologists to become community ecologists. Community ecology is undoubtedly one of the most difficult kinds of biology, but it has obvious utility as we approach oversaturation of this planet. Moreover, it is urgent that data be gathered now because so many systems are vanishing. Community ecology is also very promising. Major new advances and discoveries, potentially as important as DNA and natural selection, remain undiscovered because biologists have shied away from this discipline. So if you want to make your mark, consider working in community ecology.

COMMUNITY ECOLOGY

Community ecology is still struggling with its vocabulary. It remains a primitive and embryonic science. We do not yet have an accepted vocabulary or standard procedures. We are looking for macrodescriptors or aggregate variables that summarize some of the properties of systems (Orians 1980); this is the usual reductionistic approach. Examples of macrodescriptors include relative abundance, species diversity, trophic levels, and food webs. Food webs have been receiving considerable attention (Cohen 1978; Paine 1980, 1988; Pimm 1982; Schoener 1989; Winemiller 1989, 1990). Our choice of vocabulary constitutes a double-edged sword. The macrodescriptors we select to describe systems enable progress, but simultaneously constrain the directions our science can go, so I think it is best not to get too locked in until we are confident that we are going in the most fruitful directions. Moreover, a diversity of approaches seems desirable.

Community ecology is full of pitfalls. A major trap is that it is tempting to view an ecosystem as a sort of a superorganism, designed for smooth and efficient functioning. People make this mistake all the time. They lose sight of the fact that natural selection works at the

level of individuals and that there is a multitude of antagonistic interactions among the members of a system, for example prey-predator interactions. Natural selection operating on predators may often reduce the stability of a system, but should usually increase the efficiency of flow of energy up through the trophic levels, whereas selection operating on the prey has exactly the reverse effects. As a corollary, community-level properties of ecological efficiency and community stability may in fact be inversely related because natural selection operates at the level of antagonism between individual predators and their prey (Pianka 1987). More effort needs to be devoted to relating community-level phenomena to those at lower levels, anchored to sound thinking in terms of natural selection.

Perhaps one of the most interesting questions in community ecology is whether or not communities really possess some kind of emergent properties that are more than mere statistical expressions of the component parts. The latter sorts of phenomena have been termed "epiphenomena." One example of a truly emergent property would be a situation in which patterns of resource utilization among consumers in a system are co-adjusted with one another so that species A eats a lot of food-type X, but species B eats only a little of X and a lot of food-type Y, which in turn is not eaten by A. If this sort of complementary pattern permeates the whole system, then the system is organized and has some sort of structure. If we could remove a species, there would be a hole in the tapestry that would reflect what that species does (in fact, such an ecological vacuum might be quickly filled by shifts in patterns of resource utilization of the other species in the system).

Like scientists in general, many community ecologists gravitate towards reductionism and so they tend to approach communities from the bottom up. I would like to make a case for trying to approach communities holistically from the top down. We need the microscopic experimental approach but we should also examine other approaches. As a plant ecologist, Tilman (1987), recently stated: "Must plant ecologists manipulate the densities of every species of plant, every soil bacterium, every fungus, every nematode, every herbivore, etc., and establish the effects of each manipulation on population densities and/or growth rates of all other species just to determine whether plants are actually competing with each other? Such an approach is so complex as to be ridiculous; yet that is the approach that a purely phenomenological perspective seems to require." Tilman threw up his hands at the complexity of entire natural communities. Many reductionistic microscopic community ecologists have done just that.

In the symposium on amphibian community ecology at the First World Congress of Herpetology, we learned about the biology of small groups or sets of species. An example is the work of Hairston (1987) on salamander guilds. In a book review entitled "Putting the Species Back into Community Ecology," Pimm (1987) put it this way: "Community ecology is becoming the ecology of guilds rather than the ecology of communities." Small pieces of a complex system may well lack important properties inherent in the intact system. I propose to consider something in between the ecosystem systems approach and the guild ecology of microscopic community ecologists, and that is community ecology of entire assemblages, subsets of the whole community, but larger than just guilds.

Recently Schoener (1986) argued that in the future, community ecology will consist of a collection of theories, each with its power of prediction for a limited subset of species under specific environmental conditions. This kind of sentiment emerges from the microscopic perspective on communities. In my

opinion, we cannot afford to neglect diverse, complex systems just because they are intractable. We must make some attempt to deal with these phenomena holistically, even though they are very complicated. A great deal remains to be learned about community structure, even in the best-studied systems (Menge and Farrell 1989).

An example of these phenomena is a food web that involves 11 lizard species in the Australian desert that I put together from part of my own research (Figure 3). Aquatic food webs that Winemiller (1987) deduced for a fish assemblage in Venezuela are shown in Figure 4. In complex networks of interacting species, the numbers of indirect interactions (Kerfoot and Sih 1987), that is, interactions that require path lengths of more than one, go up exponentially with species diversity (Patten 1983). Of course, direct interactions potentially increase faster and faster with more species. Whereas direct interactions are readily understood, indirect interactions can lead to counterintuitive situations that have been called, for example, "apparent competition" (Figure 5b; Holt 1977). When a single predator has two prey species and a removal experiment is performed on one of the prey, the predator loses food, decreases in density, and hence decreases its predation on the other species. A naïve experimental ecologist might interpret such a response as competition when it is not competition at all! Other indirect interactions involve more than just two links (Figure 5). One

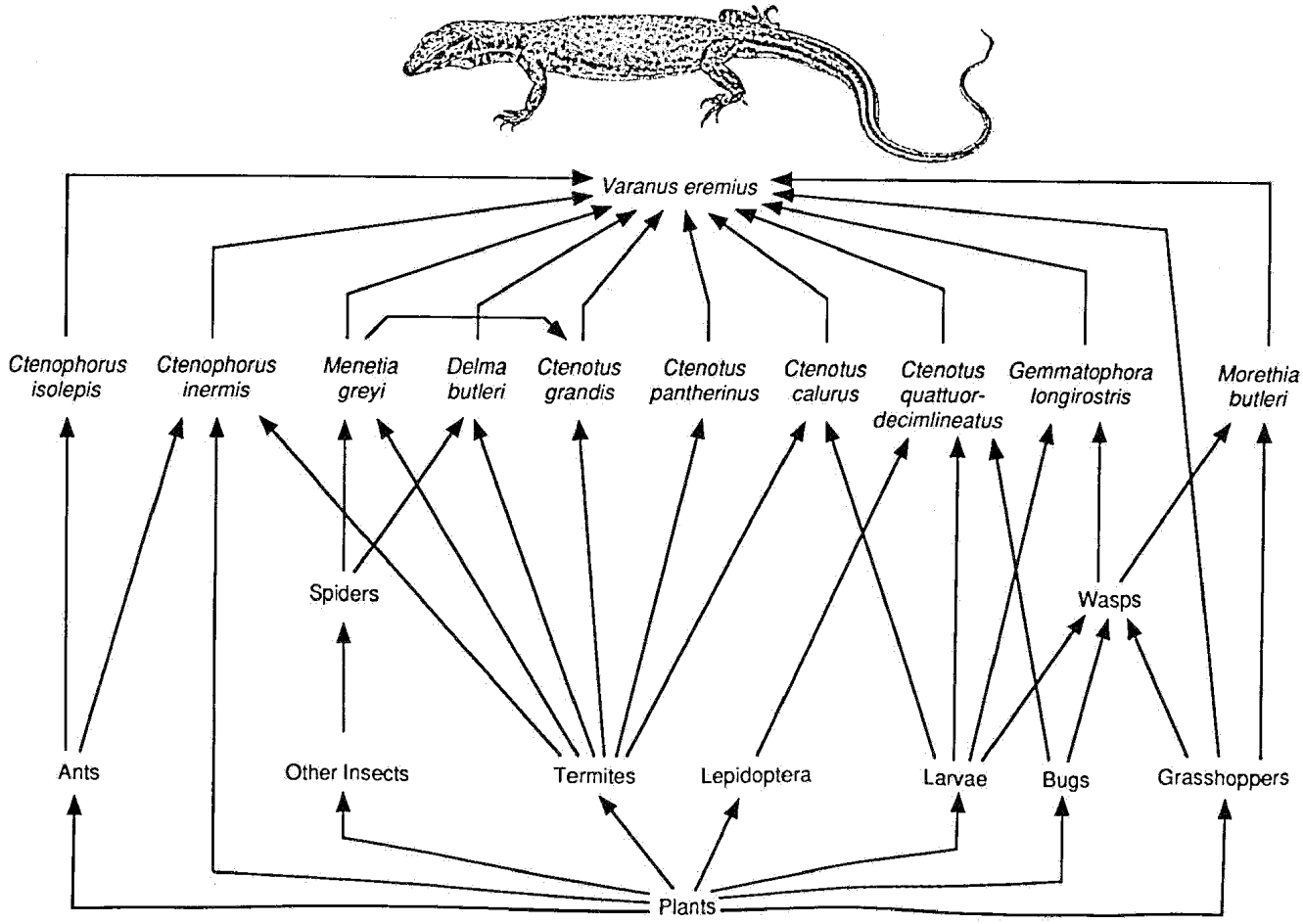


FIGURE 3. Part of the food web in an Australian sandy desert. The top predator, *Varanus eremius*, is a pygmy monitor lizard, which eats ten other species of lizards and grasshoppers. Each of the latter in turn have diets dominated by various sorts of arthropods or plants. (After Pianka 1988.)

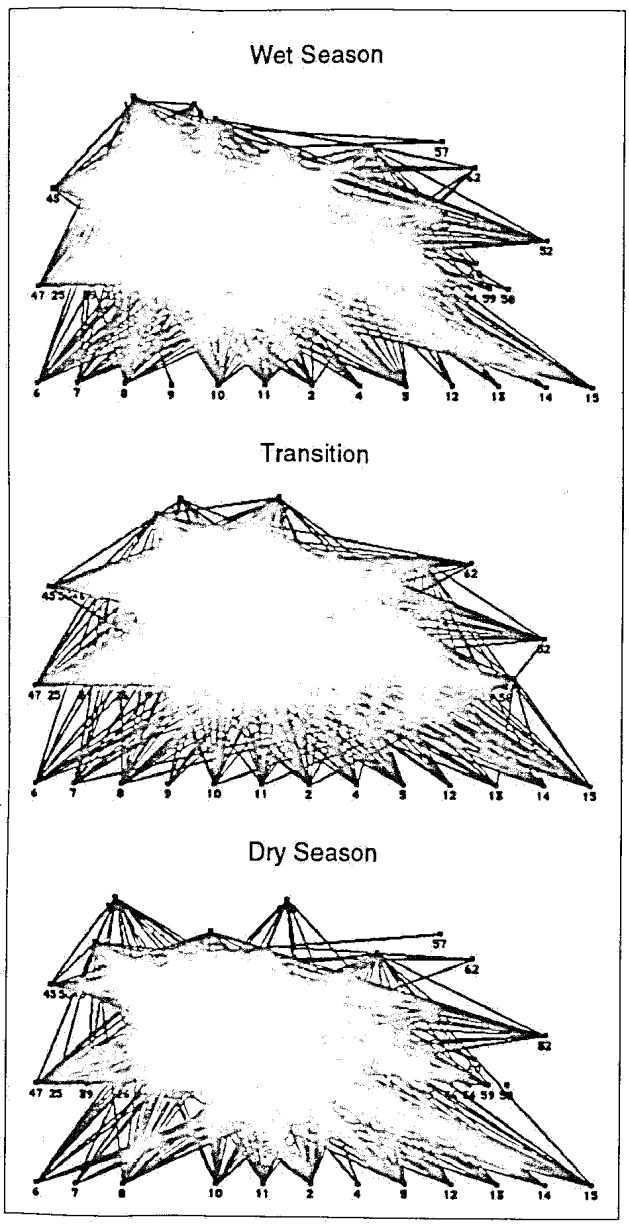


FIGURE 4. Food webs during three seasons in a neotropical aquatic system at Caño Maraca in the lowland Llanos of Venezuela. (After Winemiller 1987.) Species are represented with numbers at nodes (not all species are present during all seasons).

such interaction, which I find most interesting, is illustrated in Figure 5d; two consumers are not competing or interacting directly in any way, but because their prey are competing at the next trophic level down, a positive apparent mutualism emerges between the two consumers that has been called facilitation or indirect mutualism (Vandermeer 1980).

Still other kinds of indirect mutualism can occur horizontally and vertically, such as competitive mutualism (Pianka 1981; Figure 5c) and food-web or food-chain mutualism (Figure 5e). Ecologists have only recently become aware of indirect interactions; for too long we have been overly simplistic and classified all interactions between species just into simple pairwise interactions (Bender et al. 1984; Brown et al. 1986; Pianka 1987).

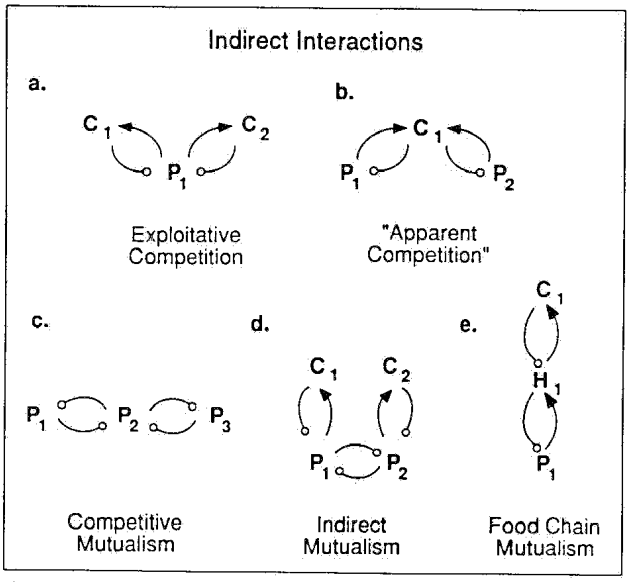


FIGURE 5. Indirect interactions in communities. (a) Two consumers sharing a common prey may compete indirectly via classical exploitation competition (resource depression). (b) Two prey species may only appear to compete, because if either increases, a shared predator also increases, which operates to the detriment of the other prey population (Holt 1977). (c) Three species's populations at the same trophic level, arranged so that one species, P_2, is sandwiched between two others. Populations P_1 and P_3 are indirect mutualists because each inhibits the other's competitor—P_2 (Pianka 1981). (d) A more complex four-species system that results in an indirect "mutualism," or "facilitation" (Vandermeer 1980). In this case, populations C_1 and C_2, which do not interact directly, but consume different prey species, interact indirectly because their prey compete: if consumer C_1 increases, its prey P_1 decreases, which in turn reduces competition with P_2, allowing an increase in this second prey population (P_2) and providing more food for consumer species C_2. (e) Three species's populations at three trophic levels: the plant P_1 and the carnivore C_1 are indirect mutualists because they share an herbivore H_1. Numerous other sorts of indirect interactions are also possible. (Modified from Pianka 1988.)

We need a way to take an entire multidimensional system, or a complex network, and reduce it to some kind of a graphical state in which we can begin to appreciate the structure and organization of the entire system. Loehle (1987) said that "the mere attempt to define phenomena operationally can dramatically increase theory maturity." I will explain, very concisely, a promising hybrid approach that Kirk Winemiller and I have developed to compare his aquatic systems with my desert systems (Winemiller and Pianka 1990).

Winemiller (1987) worked on neotropical fish in South and Central America. (I will consider some of his fish systems briefly below.) He recently returned from Zambia, where he studied similar but independently-evolved ichthyofaunas. The resulting intercontinental comparisons are most instructive (Winemiller 1991). Here I can only skim over our approach and show a few results; for a full treatment, see Winemiller and Pianka (1990). This approach adopts a holistic perspective on a complex assemblage of interacting species and endeavors to represent the entire assemblage graphically to detect patterns of organization in that system.

METHODOLOGY

Our raw data are called resource-utilization matrices. Although some people reject the whole approach of resource partitioning, we maintain that a resource matrix contains a great deal of vital information about a system. It identifies quantitatively which species eat which other species, as well as which species are potential competitors because they share common foods. A resource matrix thus describes the food-web structure of the system.

Considerable tedious work is required to put together a satisfactory resource matrix. Statistical samples of all the species in the system must be collected; if the system is changing in time, this needs to be done quickly; to follow changes in the community through time, adequate samples at different times are necessary. Entries in the resource matrix are used to estimate probabilities. These vary between zero and one, reflecting the probability that a given consumer species, called 1, will use a particular resource state, called 2. A portion of these utilization probabilities, or u_{ij}'s, in the matrix will obviously be zeros because some consumers will not be using particular resources. Without going into all the detail of the various sorts of probabilistic elements that one can compute to enter into such resource matrices, I will briefly discuss the concept of electivity.

Simple dietary proportions, or p_i's, weight uncommon or very abundant resources disproportionately. Ivlev (1961) suggested resource utilization should somehow be standardized in terms of relative availabilities. As it turns out, resource availability is a very difficult problem, not easily measured in the field. Insects can be sampled with sweep nets, DeVac vacuum cleaners, tanglefoot sticky traps, pit traps, or Berlese funnels; each technique yields very different results. Some insects are simply more easily pit trapped than others, whereas others are captured by Berlese funnels more efficiently than are others, and so on. Péfaur and Duellman (1980; Duellman, pers. comm.) studied Andean amphibians and reptiles from Colombia south to Argentina. They fenced study plots and collected all frogs and squamates (lizards and snakes) inside these plots; all the conspicuous insects were also collected, and saved with the intention of using these as standards to compare with the stomach contents. They actually collected only a very few of the insect species that were eaten by the amphibians and reptiles—only about 10%, in fact (Duellman, pers. comm.). Incredibly, 90% of the insect species that were in stomachs were, in fact, not even collected by diligent humans! It is a gross and dangerously

misleading oversimplification to accept the idea that there exists a single resource vector that describes a system. Each species experiences its own resource availabilities, which depend to some extent on how that species uses space and time, and its sensory capacities, as well as its behavior and foraging mode.

Various operational "solutions" to this problem have been proposed, although all have their limitations and shortcomings. Colwell and Futuyma (1971) suggested a technique that weights resources in proportion to their use in the overall system. We use a convenient and simple variant proposed by Lawlor (1980*a*) that exploits the resource totals in the resource matrix as our measure of resource availability. This constitutes a sort of bioassay. In a system of a hundred species, the diet summed over all the component species represents an estimated resource availability vector. This is used to compute probabilistic analogues of electivity and an analysis can proceed that is unbiased by resource availability (Winemiller and Pianka 1990).

One of the classic papers in community ecology was published in 1977 by Robert Inger and Robert Colwell on Thailand amphibians and reptiles. In that paper they pointed out that there is no consensus as to how to approach community ecology. Inger and Colwell (1977) said that there is "no standard protocol for community ecology." That statement is still true today, more than a dozen years later.

Even so, Inger and Colwell (1977) made a giant step. They suggested a nearest-neighbor approach for looking at communities; each species' overlap with every other species is ranked from the closest neighbor in niche space to those increasingly more distant. These generate monotonically declining curves for all the species in the system (for an analogous graph of Botswana lizards, see Figure 6). Some species have high overlap well out into niche space, whereas overlap in others falls off rapidly (such consumers are very distinct and have low overlap with most of the other members of the system).

The hybrid approach that Winemiller and I developed uses simply the mean overlap at a given rank across all species in the system. A system in the Kalahari desert involving 15 species of lizards is depicted in Figure 6. This system is also represented in Figure 14, although with a single curve, and that one curve is simply the arithmetic average over all 15 species at each rank in niche space.

NULL MODELS

Now we must get a bit more abstract. Another promising technique involves what are called null models (Colwell and Winkler 1984). One of the big challenges is to find something with which to compare a given community. It is extremely difficult to compare a system with someone else's system; that is, in fact, what provoked us to devise these techniques, so we could compare the fish with the lizards. Sale (1974) suggested scrambling the elements of a resource matrix according to rules that create what I have since come to call pseudocommunities (Pianka 1986). These are then compared with the prototype so that we can look for differences in how the original system is organized. Sale's algorithm involved scrambling all the utilization coefficients, whatever their values are for each consumer in the system (zeros or positive). So one simply takes the first consumer and randomly rearranges all its elements. Rearranged utilization probability u_{31} could fall with equal probability into any slot in the utilization vector of that species and so would u_{11}. The nice thing is that, with a computer, one can easily perform this rearrangement a hundred times and with the use of the bootstrap approach and Monte Carlo statistics, can generate a distribution against which the observed data can be compared (Felsenstein 1985). The beauty of such

an approach is that non-independence can be handled statistically—unlike the familiar parametric statistics, independence is not assumed or required (Pimm 1983). Thus one can actually do statistical analyses and say whether or not any differences are significant.

About six years after Sale's work, Lawlor (1980*b*) suggested a slightly different algorithm, which turned out to be equally instructive: Lawlor's algorithm leaves the zero structure of the resource matrix intact. So, if consumer 1 does not eat resource state 3, a zero must remain in cell u_{31}; it is frozen and not allowed to change. Elements in the resource matrix are scrambled, but only among the resources that are actually used by a given species. (We call Lawlor's method the "conserved-zero" approach and Sale's method the "scrambled-zero" algorithm because it destroys the zero structure.)

BENCH TESTS

To intelligently exploit these techniques on our real fish and lizard systems (Winemiller and Pianka 1990), we first constructed a test set of hypothetical model systems that had an understandable, known structure. We built model systems both with and without guilds and "bench tested" our methodology on these. The three systems of two guilds of equal size that are depicted in Figure 7—five species in each—are simple little model systems that we

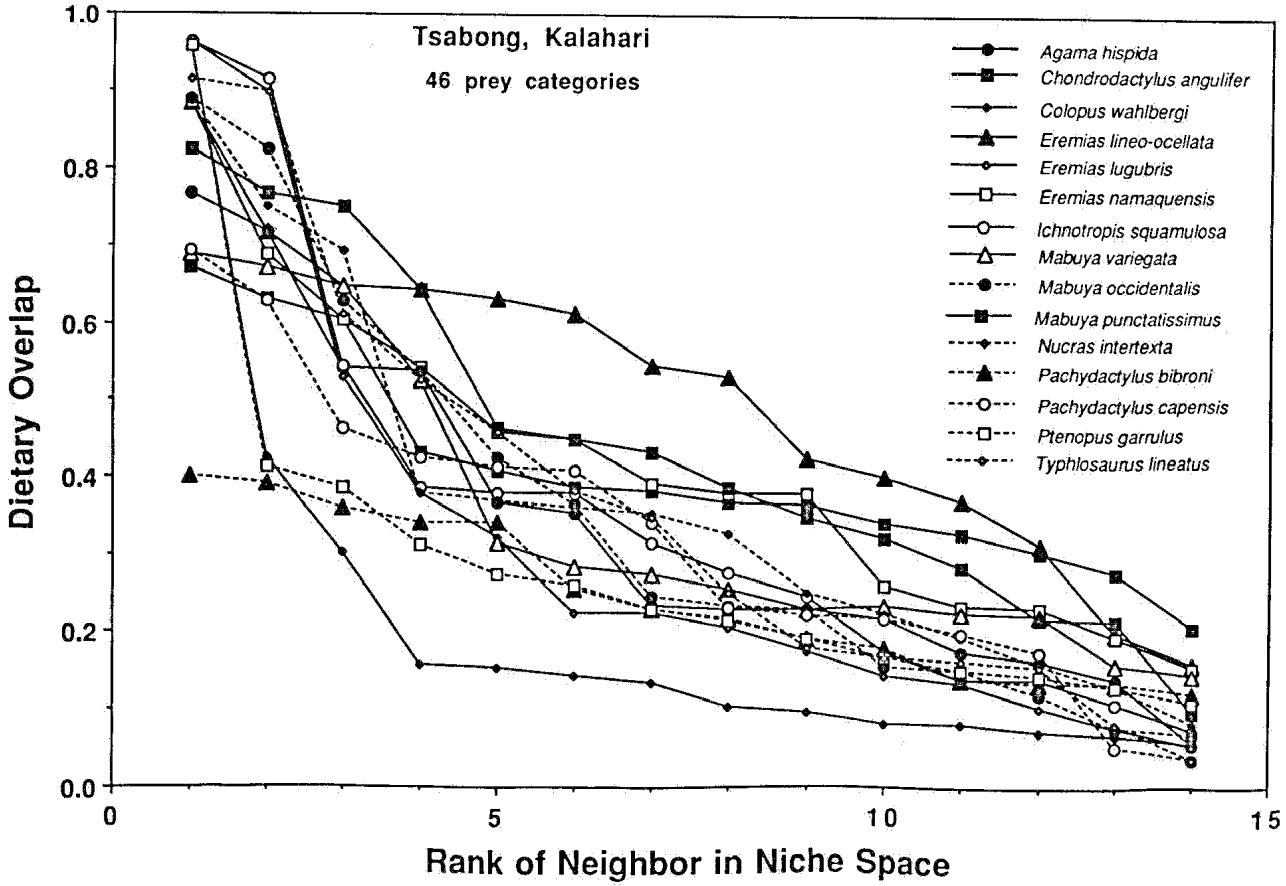


FIGURE 6. Plots of dietary overlap with niche neighbors ranked for each lizard species at Tsabong, Botswana. Dietary overlap declines at more distant ranks, but average slopes exhibit large interspecific variation. Overlap at distant ranks is variable in this lizard system. Steep negative slopes indicate relatively unique diets and ecological similarity with very few other species, whereas shallow slopes indicate high or intermediate ecological similarity with many species. (From Winemiller and Pianka 1990.)

used in order to see the effect of randomization algorithms. At the top, there are two guilds with very high, almost total, overlap. At the bottom, there are two guilds with low overlap. In the middle, overlap is intermediate. When the zeros are scrambled, of course, guild structure is destroyed and the scrambled-zero algorithm results in increased overlap at distant ranks in the niche space. If a significant proportion of pseudo-communities lie above the original system (the prototype), in effect they "float," indicating that niche segregation was reduced or destroyed when the resource matrix elements were scrambled. At close-in ranks, pseudo-communities "sink" because guild structure is diminished by scrambling utilization coefficients.

We assembled another set of three systems with guilds of different sizes; these behaved

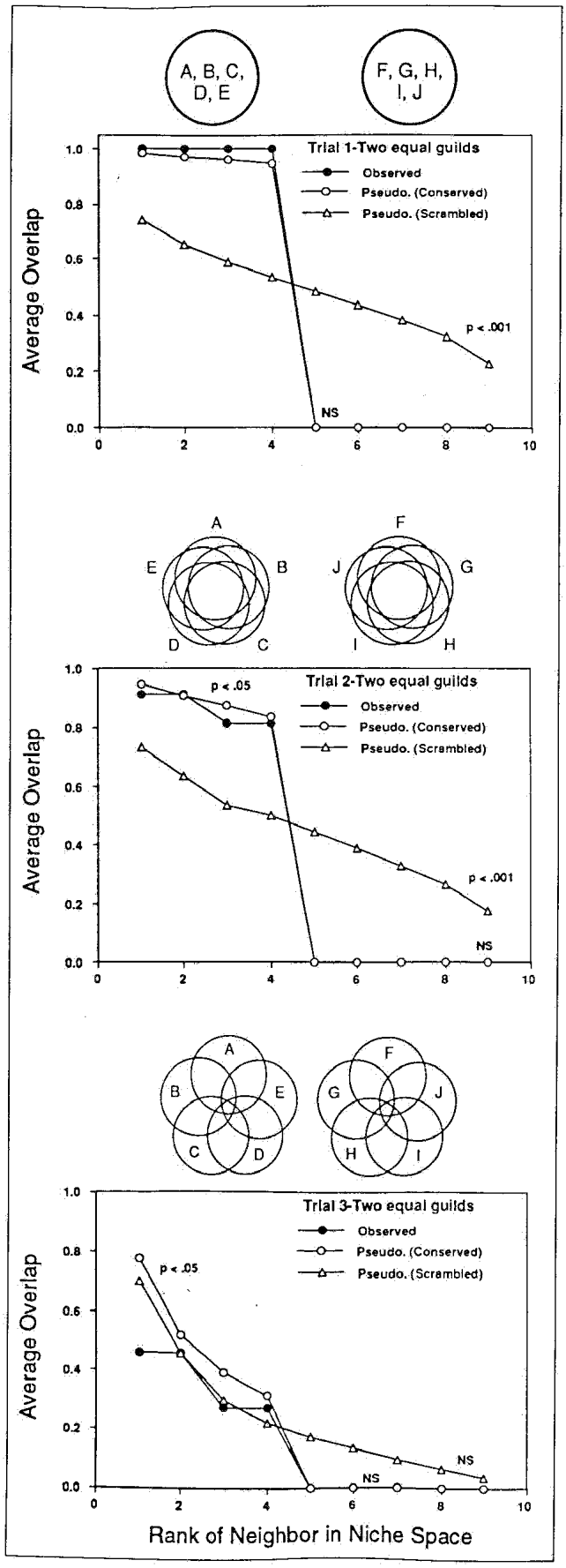
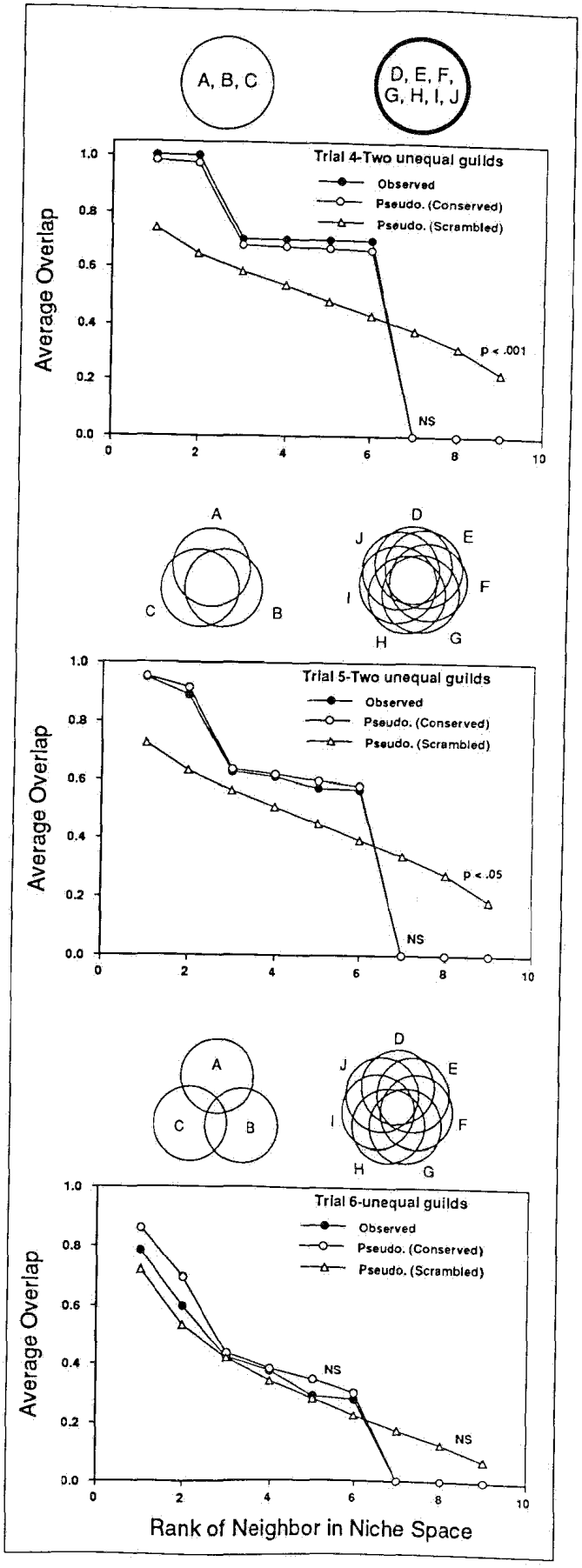


FIGURE 7. Plots of average niche overlap against rank of niche neighbor for three model assemblages with guild structure and the same plots using means from 100 randomizations based on two algorithms (resource matrices for each model system are given in Winemiller and Pianka 1990). Set-theory representations of the systems are depicted above each Colwellian nearest-neighbor plot. For systems with high overlap, scrambled-zero pseudo-communities fall below observed systems within guilds, but lie above observed systems at more distant between-guild ranks. The Trial 1 (two guilds, high overlap) plot shows the observed system exceeding both pseudo-community overlaps at the first 4 out of 9 ranks. The Trial 2 (two guilds, moderate overlap) plot shows 4 of 9 observed overlaps exceeding pseudo-community overlaps based on the scrambled-zeros randomization algorithm. Trial 2 conserved-zero pseudo-communities fall above the observed system for 3 of 9 ranks, indicating marginal resource segregation. Scrambled-zero pseudo-communities sink at close-in ranks, but float significantly at distant ranks in niche space as a result of destroying guild structure. In Trial 3 (two guilds, low overlap), conserved-zero pseudo-communities float significantly at the first four ranks in niche space reflecting segregation, whereas no other differences are significant. Conserved-zero probabilities are based on the fraction of randomized means exceeding observed-rank means. Scrambled-zero probabilities are based on the fraction of randomized means below observed-rank means. (From Winemiller and Pianka 1990.)



somewhat the same (Figure 8). We also put together systems like these without any guild structure, but with resource partitioning (Figure 9). It became harder to get pseudo-communities to float, although some conserved-zero pseudo-communities did float, which we interpreted as evidence of niche segregation.

We were also interested in the phenomenon of "core" resources. Both Winemiller's fish and my lizards exploit certain core resources extensively. Among the lizards, these are termites and ants—especially termites. Among the fish, mayflies constitute a core food resource. So we created some systems with extensive or total overlap on certain core resources and some systems with unique resources that were used by each species and that were partitioned (Figure 10).

To sum up the bottom line on these algorithms: when consumers piled up on a certain resource state (core resources or guilds in which everything within a guild ate the same things), the scrambled-zero algorithms tended to sink and fall below observed levels. When resources are partitioned, however, conserved-zero pseudo-communities tended to be above the observed system (i.e., they "floated").

FIGURE 8. Plots of average niche overlap against rank of niche neighbor for three model assemblages with two guilds of different sizes and the same plots using means from 100 randomizations based on two algorithms (resource matrices for each model system are given in Winemiller and Pianka 1990). Again, for systems with high overlap, scrambled-zero pseudo-communities fall below observed systems within guilds, but lie above observed systems at more distant between-guild ranks. The Trial 4 (two distinct guilds of different sizes, intermediate overlap) plot shows the observed system above both types of pseudo-communities at close-in ranks. Scrambled-zero pseudo-communities tend to sink close-in but float significantly at distant ranks in niche space, a result of destroying the guild structure. Neither set of pseudo-communities differs from the observed system in Trial 6 (unequal-sized guilds with low overlap). (From Winemiller and Pianka 1990.)

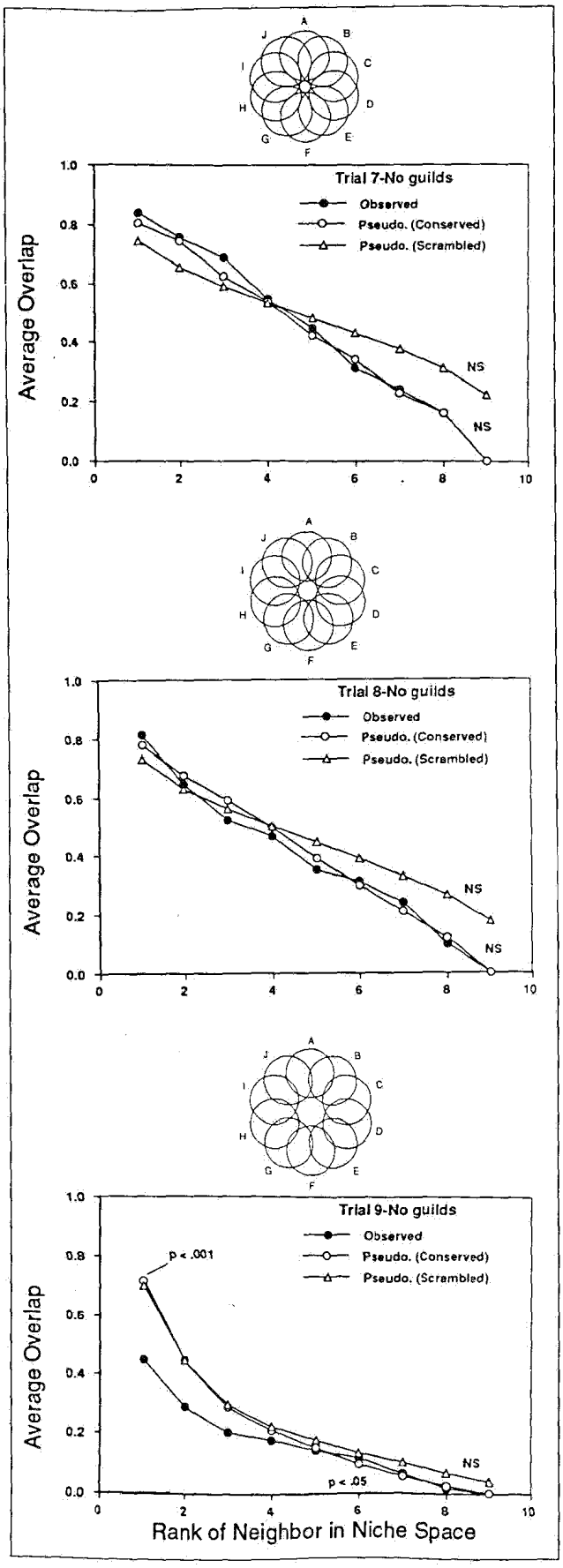


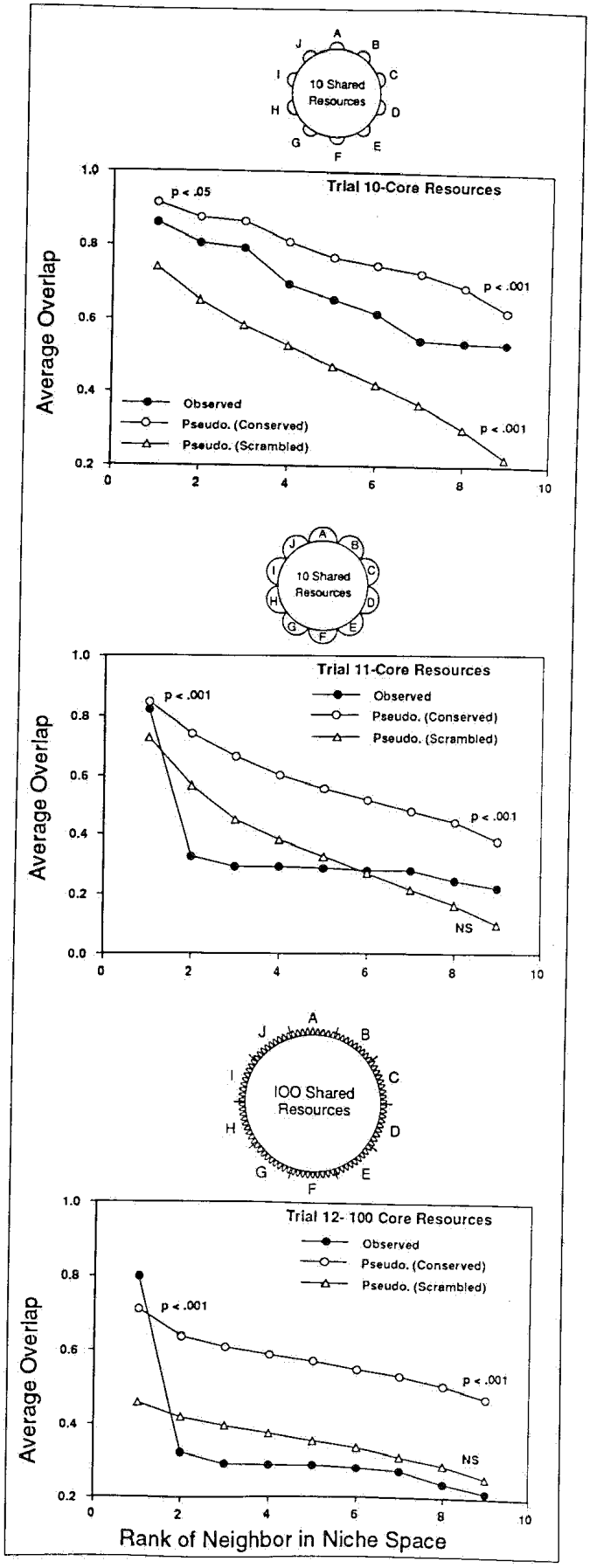
FIGURE 9. Plots of average niche overlap against rank of niche neighbor for three model assemblages with no guild structure and the same plots using means from 100 randomizations based on two algorithms (resource matrices for each model system are given in Winemiller and Pianka 1990). Pseudo-community overlaps at most ranks do not differ significantly from the observed system when overlap is high, but do tend to float at close-in ranks when resources are partitioned and observed overlap is low (Trial 9). (From Winemiller and Pianka 1990.)

RESULTS FROM REAL SYSTEMS

My colleague, Kirk Winemiller, studied ichthyofaunas of aquatic systems in Venezuela and in Costa Rica. One of his study sites has more than 80 species of fish in it over the course of an entire annual cycle. Winemiller discovered how to collect virtually an entire freshwater aquatic assemblage. In one seine haul through Caño Maraca during the dry season, he and I captured over a thousand fish of dozens of species—plus a "bonus" of a couple of large caimans! His sample sizes are on the order of 300–500 specimens. Winemiller could not examine the stomachs of all these fish, but went through statistical subsamples and separated his data into wet- versus dry-season resource matrices. Prey content—usually insect orders—was estimated by volume to the narrowest discriminatory abilities possible, given our own expertise.

We examined 18 different resource matrices, with two or three from each of eight sites: a wet and dry season for each of four fish sites and microhabitats plus diet matrices for each of four lizard sites. Numbers of fish species on these sites varied from 19 to 59 and numbers of lizard species varied from 15 to 39. We had between 40 and 217 resource states among the sites analyzed.

One Australian desert site, an L-shaped area near Laverton, Western Australia, has 35 species of lizards. My favorite study area is Red Sands, near Yamarna Homestead in



Western Australia. I have collected 47 species of lizards there so far and expect to find several more. The hummock-grass tussock-plant growth form (spinifex) is very important in the Australian desert. These tussocks, as large as 1 m in diameter, house certain lizards that virtually never leave them. Some lizards are highly adapted to spinifex and virtually "swim" through it with ease. Each lizard collected, some 3000 in Australia and another 2000 from the Kalahari, was weighed and measured in the field, individually tagged, and then permanently preserved by injection with formaldehyde. (These specimens are all safely ensconced in major museums where they are available for systematics research. Many have been dissected by specialists interested in functional anatomy.) When the lizards are eventually taken to the laboratory, each is measured—ten different body measurements are taken for anatomical analyses—and then the lizard is dissected, its reproductive state is noted, and relative clutch mass is estimated (testicular cycles can be deduced from serial samples like this). The most important thing, for present purposes, however, is that the stomachs are removed for examination. A competent entomologist, Thomas Schultz, went through the stomach contents of the Austra-

FIGURE 10. Plots of average niche overlap against rank of niche neighbor for three model assemblages with no guilds and with consumers segregated on different core resource states, plus the same plots based on means of 100 randomizations using two algorithms (resource matrices for each model system are given in Winemiller and Pianka 1990). In trial 10 (core resources, high overlap), conserved-zero pseudo-communities float significantly whereas scrambled-zero pseudo-communities sink. In Trial 11 (core resource, intermediate overlap), conserved-zero pseudo-communities float whereas scrambled-zero pseudo-communities do not differ significantly from observed. Trial 12 (core resource, intermediate overlap, 100 resource states) shows a pattern similar to Trial 11, except that conserved-zero overlaps sink in relation to observed values at rank one (nearest neighbor), indicating that expanded resource categories are less likely to result in significant patterns of resource segregation. (From Winemiller and Pianka 1990.)

lian lizards, identifying 100,000 or more prey items to the narrowest categories possible (Pianka 1986).

Neotropical Fishes

Costa Rican fish assemblages, shown in Figure 11, were collected during the wet and dry seasons and are based on two different resource matrices (some fish species present in the wet season are not there during the dry season). Mean overlap in the observed system is indicated by the solid circles in the upper panel of each graph. Overlap at each rank in niche space is plotted, with the average similarity between consumers at the first, second, and third rank and so on. Pseudo-communities are shown with the open symbols; the conserved-zero pseudo-communities are represented by open circles and the scrambled-zero pseudo-communities by open triangles. In the lower panels of each figure, the percentage of pseudo-communities that either "float" or "sink" is plotted. In this case, sinking of the scrambled-zero pseudo-communities is interesting, as is floating of conserved-zero pseudo-communities, which reflects niche segregation. The dashed lines in the bottom panels are at 5% and 95% confidence levels, so when a pseudo-community lies above the upper dashed line or below the lower dashed line, there is a statistically significant difference between the pseudo-communities and the observed system. At close ranks in niche space, conserved-zero systems do not float, but farther out they clearly differ from observed systems and to some extent (except for the lower right panel in the figure), the scrambled-zero pseudo-communities almost invariably sink at most ranks.

Venezuelan fish float and sink even better, so to speak (Figure 12). Realize that an enormous amount of information is represented in one graph. In one case, at Maraca (top panel), data from 29,000 fish went into production of

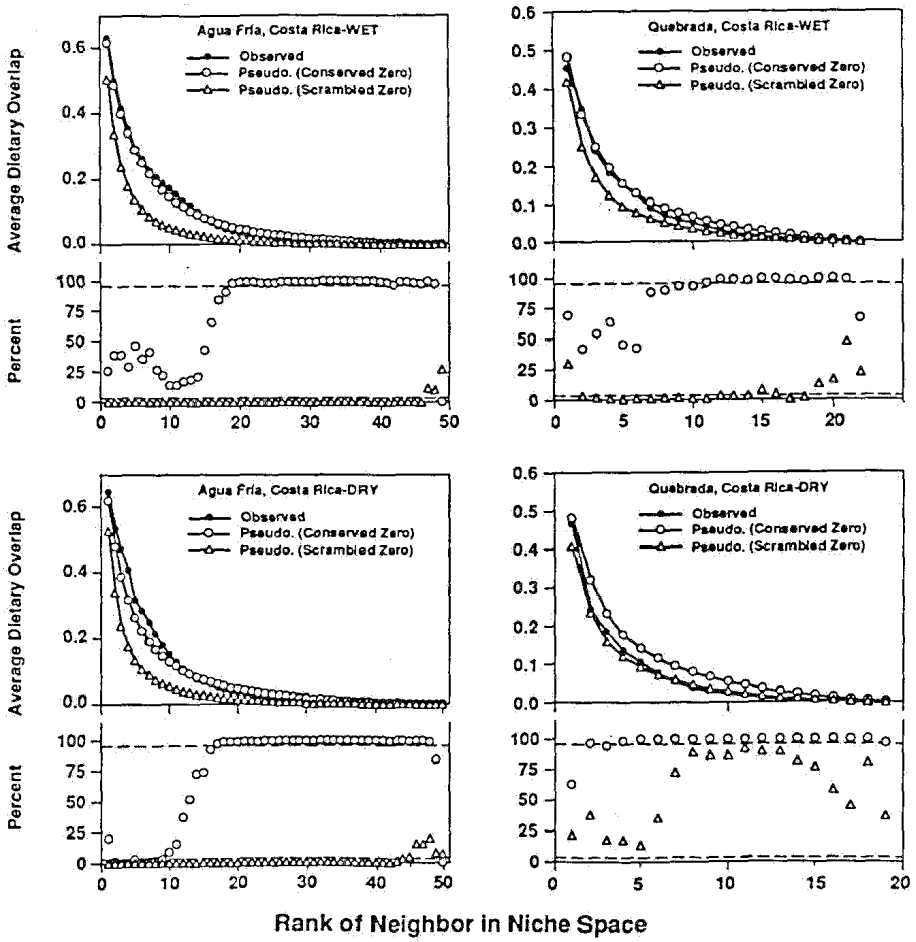


FIGURE 11. Average observed dietary overlap plotted against rank of niche neighbors for two Costa Rican fish assemblages during wet and dry seasons. Pseudo-community data are based on 100 computer randomizations of the observed prototype. The lower portion of each plot shows the percentage of pseudo-community means greater than the observed mean at each rank in niche space. Conserved-zero pseudo-community plots lie above observed levels, indicating a high degree of resource segregation. For all assemblages except Quebrada-dry, scrambled-zero pseudo-community plots fall below observed plots, indicating core resources and guild structure. (From Winemiller and Pianka 1990.)

the figure. Winemiller lived in Venezuela for a full year, collected many thousands of fish, brought them back, and spent an entire year going through the stomachs of vast numbers of these specimens. All this information can be represented on a single page with a simple graph that one can examine and interpret with a little bit of training.

These aquatic systems are highly organized, with guild structure, core resources, and niche segregation. Consumers are piled up on certain core resources, which is reflected in the sinking of the scrambled-zero pseudo-communities. Those same consumers, however, are also segregated out on those core resources that they do use, with different species using the same core resources, but with different probabilities.

Desert Lizards

Australian lizards are depicted in Figure 13. The top two panels represent microhabitats and the middle two show "standard" dietary resource matrices (19 prey categories, which are largely insect orders). The two panels at the bottom are expanded dietary resource matrices with 201 different prey categories that are represented at Red Sands, shown in the left column, and 217 prey categories that are recognized at the L-shaped area near Laverton, shown at the right. Some interesting interpretations emerge from these plots. Scrambled-zero pseudo-communities tend to sink in all cases, which indicates piling up on certain core resources and is indicative of guild structure. Conserved-zero pseudo-communities float fairly well in microhabitats, which indicates niche segregation: different species use different microhabitats and they float fairly unequivocally, except at the closest ranks at Laverton. In the middle panels, though, pseudo-commu-

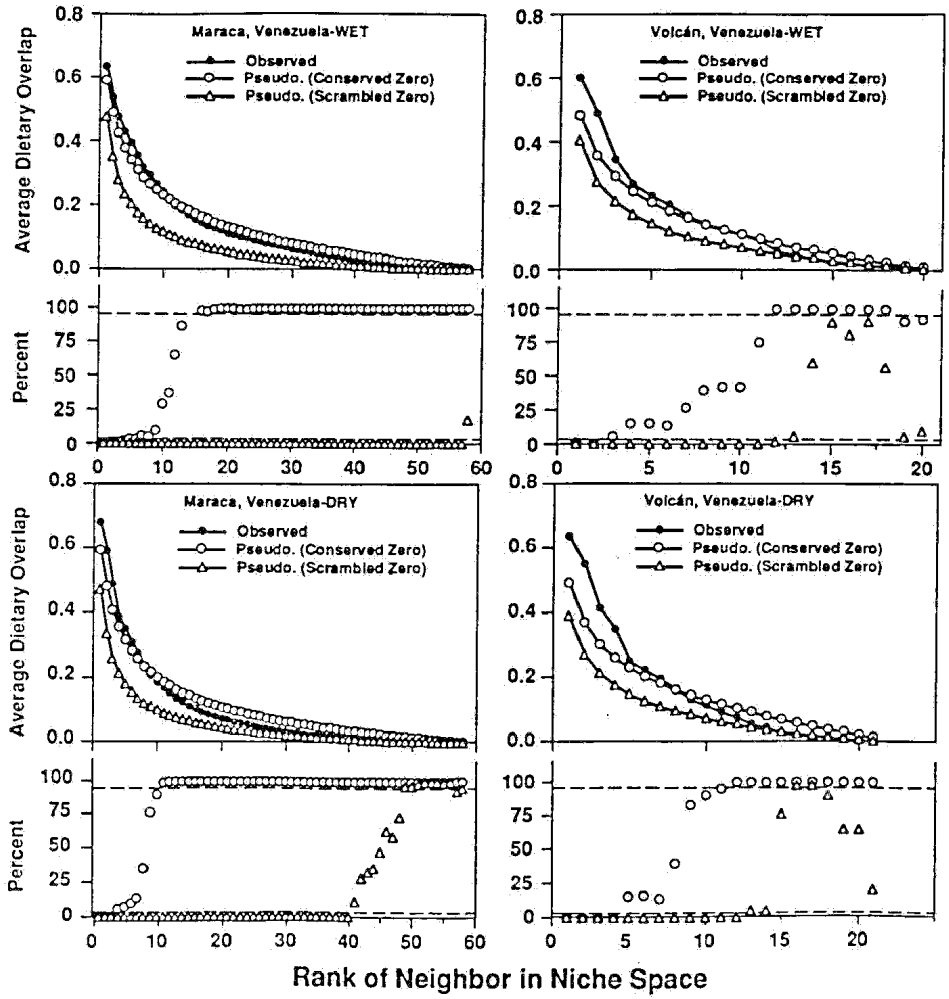


FIGURE 12. Plots of average observed dietary overlap against rank of niche neighbors for two Venezuelan fish assemblages during wet and dry seasons. Again, pseudo-community data are based on 100 computer randomizations of the observed prototype. Conserved-zero pseudo-community plots lie above observed plots, indicating a high degree of resource segregation. Scrambled-zero pseudo-community plots lie below observed plots, indicating core resources and guild structure. The lower panel in each plot shows the percentage of pseudo-community means greater than the observed mean at each rank in niche space. (From Winemiller and Pianka 1990.)

nities do not show very much floating because food resource states are too crudely differentiated, which results in a piling up of consumers on some resource states. Data for the same saurofaunas are shown in the bottom panels, but with considerably finer discrimination of prey resource states; note that conserved-zero pseudo-communities float as they did in the fish populations, indicating segregation.

Kalahari desert systems are more loosely organized than those in the Australian desert (Figure 14). There are fewer lizard species in the Kalahari and prey could not be distinguished to categories as fine as those in Australia—only 46 different prey resource states were recognized. For microhabitats, there is some hint of floating in the conserved-zero pseudo-communities at Tsabong, Botswana, on the right (Figure 14), but not at Bloukrans, South Africa, on the left (Figure 14). Examining diet (bottom panel) shows there is not much niche segregation. There is not any niche segregation at all at Tsabong, but there seems to be a little, at least at more

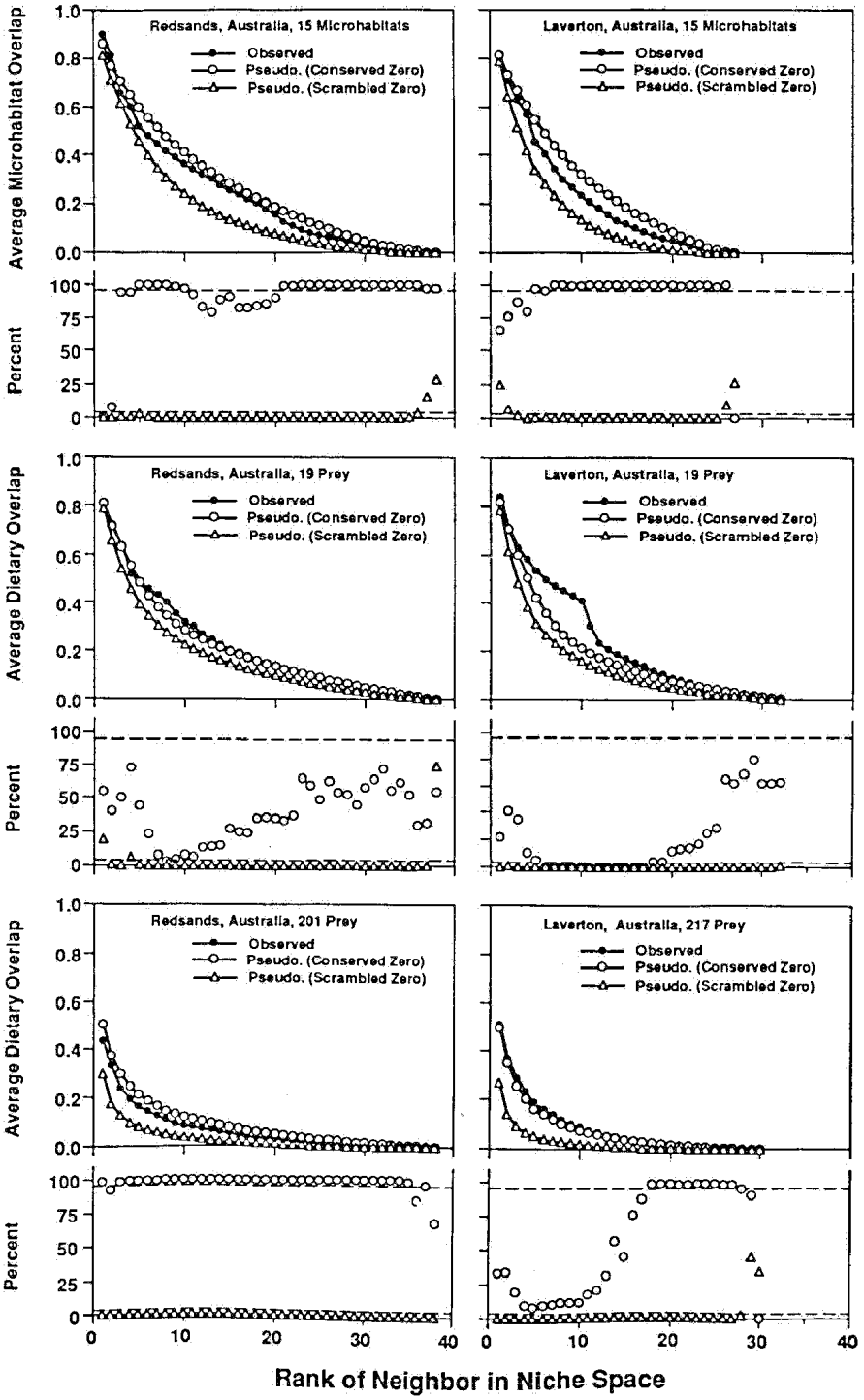


FIGURE 13. Plots of average observed overlap in microhabitat (top panels), and diet (middle panels—19 condensed resource states) and detailed prey categories (bottom panels) against rank of niche neighbors for two Australian lizard assemblages. Again, pseudo-community data are based on 100 computer randomizations of the observed prototype, and the lower portion of each plot shows the percentage of pseudo-community means greater than the observed mean at each rank in niche space. Except for condensed-prey resources, conserved-zero pseudo-community plots float above observed levels at some but not all ranks, indicating significant resource segregation at these ranks. In each case, scrambled-zero pseudo-community plots fall below observed plots, indicating significant guild structure. (From Winemiller and Pianka 1990.)

distant ranks, at Bloukrans. All in all, the systems we examined tended to be fairly highly organized. This technique should facilitate analyses of other systems and allow comparisons with our own.

Laurie Vitt (pers. comm.) has collected comparable data for the diets of lizards in a semiarid habitat in Brazil known locally as the "caatingas." Sixteen species of lizards, all in different genera, occur there (three species are very rare). Recognition of 136 prey categories (insect families for the most part) allowed the construction of a resource matrix describing the 13 dominant species in this system. A preview of this study (Vitt, in prep.) shows that overlap is very low or non-existent between almost all pairs of species. Both conserved-zero and scrambled-zero pseudo-communities float at all ranks in niche space. The caatingas saurofauna system is extremely highly organized in terms of niche segregation, but lacks any guild structure.

FIRE SUCCESSION IN INLAND WESTERN AUSTRALIA

The importance of spatial scale has been neglected in traditional ecology, although not in the emerging field of landscape ecology. While the implications of the landscape on ecology have long been appreciated, only recently have quantitative methods of study been exploited. In the past, ecologists, including myself, have focused on local-level processes. Larger scale regional factors also control local phenomena. Local species richness may often be a consequence of regional processes (Shmida and Wilson 1985). Relatively little empirical attention has been given to the interaction between these two levels. Unfortunately, few complete closed regions remain, unfragmented by human activi-

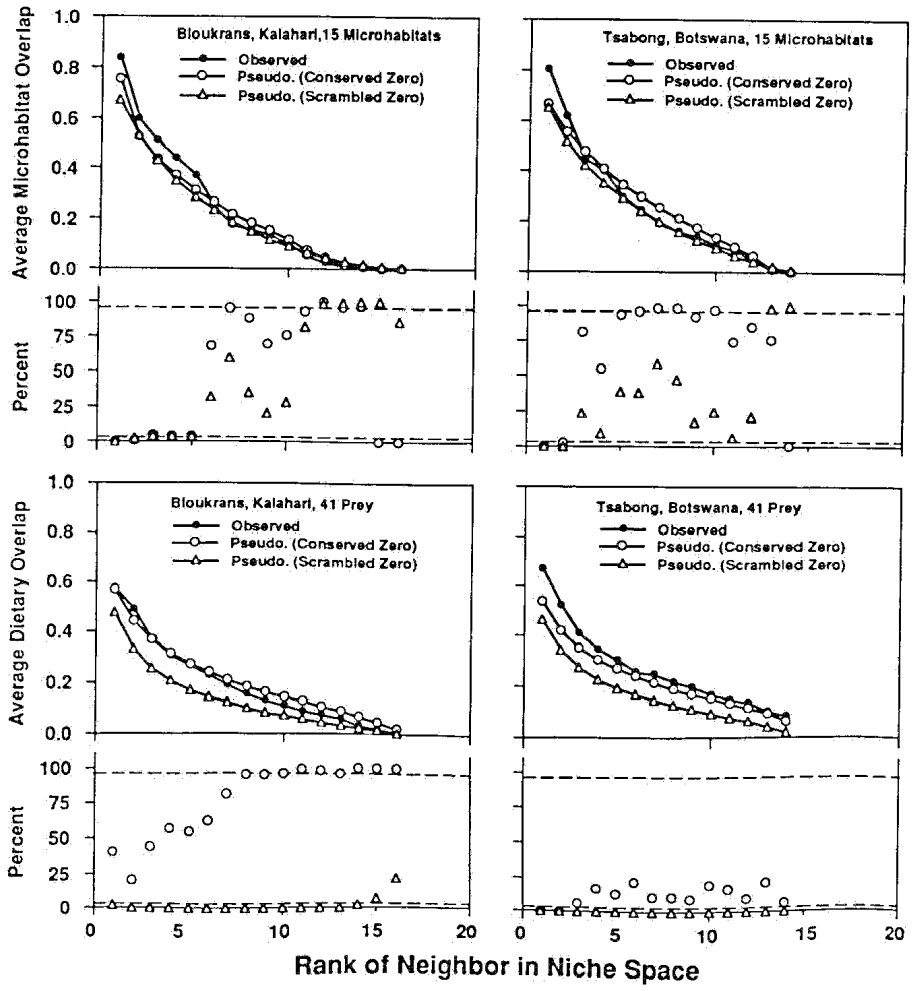


FIGURE 14. Average observed microhabitat overlap based on detailed resource states (top panels) and average observed dietary overlap (bottom panels) plotted against rank of niche neighbors for two Kalahari lizard assemblages. Again, pseudo-community data are based on 100 computer randomizations of the observed prototype and the lower portion of each plot shows the percentage of pseudo-community means greater than the observed mean at each rank in niche space. Conserved-zero pseudo-community plots lie above observed levels at some ranks in 3 of the 4 plots, indicating resource segregation. In each case, at some ranks scrambled-zero pseudo-community plots sink below observed, reflecting core resources and guild structure. (From Winemiller and Pianka 1990.)

ties, in which regional and local phenomena can be studied simultaneously. I am undertaking such a study in the uninhabited Great Victoria Desert of Western Australia, an area with an extremely high diversity of lizards.

Fires were once a major agent of disturbance in all grassland and semidesert biomes, including the North American tall grass prairies. Most of these ecosystems have now been reduced to mere vestiges, and controlled burning, fire control, or both are practiced by humans almost everywhere. The inland Australian desert is one of the last remaining areas where wildfires remain a regular and dominant feature of an extensive natural area largely undisturbed by humans. An important fire-succession cycle, which generates spatial and temporal heterogeneity in microhabitats and habitats, is evident in this region. Habitat-specialized species can become extinct within a given habitat patch (a fire scar), but metapopulations persist in the overall system by periodic reinvasions from adjacent or nearby patches of suitable habitat of different age. An ecological and evolutionarily stable equilibrium is reached between "source" and "sink" habitats (Pulliam 1988). Such regional processes promote local diversity.

Precipitation is the driving variable in this system, which is being studied, both at the local level in the field in Australia and at the regional level, using aerial photographs of fire scars and multispectral satellite imagery by Melba Crawford at the Laboratory for Remote Sensing at the University of Texas. High-resolution satellite imagery of these areas, which has been collected since 1972, offers a powerful way, heretofore underutilized, to acquire regional-level data on the frequency and phenomenology of wild fires, and thus the system-wide spatial-temporal pattern of disturbance.

Many of the digital satellite data have been acquired by LANDSAT, but they remain archived on magnetic tape and unprocessed, and are thus exceedingly expensive and therefore essentially unavailable without substantial financial resources. A complete analysis of wild fires of the Great Victoria Desert region will require at least 100 images. Imagery is being purchased and will be analyzed to detect burned areas. Spectral and spatial statistics will be computed for hundreds of fires through time, and the probability that a given area will be burned will be estimated. Other data to be collated for each fire include date, location, area, perimeter, compass direction (of burn and prevailing wind), ground-cover characteristics, extent of reticulation, and various fractal dimensions. Age and size distributions of burn patches will be estimated. Supporting imagery from other grassland areas, particularly the Kalahari semidesert of southern Africa, will be acquired and used for comparative purposes (fires in the Kalahari do not appear to reticulate to as great an extent as they do in Western Australia).

Chronosequences of remote imagery will be correlated with historical weather data. Both past climate (cumulative precipitation since the last fire) and the present state of the vegetation and fauna of unstudied sites will then be inferred from multispectral reflectance properties. Although a great deal more remains to be learned, it may ultimately prove feasible to monitor habitats and biotic diversity in this arid region from satellites in space.

Field work is currently underway on the ground to document rates of closure of spinifex, to map vegetation structure, and to determine which animal species are present and in what abundance at various stages following burns. Low-level aerial photography is being acquired and will be digitized, georeferenced, and analyzed to make detailed maps of vegetation structure for use in computer simulations of fire dynamics. Vertebrate faunas, arachnids, and insects—in particular, foods

eaten by lizards—will be compared at recently burned sites with those at various stages of post-fire recovery to collect preliminary data for modeling aspects of the dynamics of the fire-succession cycle. Mature spinifex sites have been selected for long-term monitoring. After their faunas have been sampled and low-level aerial photography of the spatial distribution of combustibles has been acquired, these study sites will be burned under varying wind conditions. Fire scars will be photographed and "burns" will be simulated on the computer to mimic observed fire geometry. Precipitation, rates of accumulation of combustibles, and the insect and vertebrate faunas of these study sites will be monitored roughly every other year for the next decade to collect more precise data on the fire-succession cycle.

A major goal of this study is to obtain baseline data on temporal patterns, spatial structure, and distribution of disturbances. These data will form the backdrop for a more detailed study of the population dynamics and dispersal abilities of species. Such data on the component species will be fitted into the overall spatial-temporal mosaic in an effort to explain the persistence of this diverse desert fauna. Ultimately, I plan to model the entire Great Victoria Desert region as a dynamic habitat mosaic so as to understand mechanisms of coexistence of its component species and the effects of fire disturbance in maintaining lizard diversity in this region. Faunas of unstudied sites will be predicted by extrapolation, allowing direct tests of models. Controlled burns may also prove to be useful.

CONCLUSIONS

Community ecology has for too long been perceived as repugnant and intractably complex by reductionistic population ecologists. As a result, the discipline has been neglected and now lags far behind the rest of ecology. As we approach oversaturation of this planet, we will soon be needing all the ecological understanding and wisdom that we can muster. No longer can we afford to remain ignorant of the principles and factors governing the structure and function of entire systems of interacting species. Community ecology is not for the timid, but its serious students may well be rewarded with major new advances and discoveries every bit as exciting and important as DNA and natural selection.

I would like to close with a plea for tolerance of community ecology. Allow the discipline to try to catch up with the rest of biology, which has enjoyed such a head start. I would particularly like to ask those community ecologists who adopt the microscopic approach, that is, "experimental" community ecologists, to be tolerant of community ecologists trying to study entire assemblages and who are adopting a more holistic and "descriptive" approach to communities. We must seek and maintain dialogue and mutual respect as we work towards integrating our divergent but complementary approaches.

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