VII.13 Grasshopper Communities and Methodology

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Grasshopper populations do not exist in an ecological vacuum. Instead, individual species populations interact with several other species, other individuals, other herbivores, a range of potential host plants and many natural enemies. In western North America, 30 to 50 grasshopper species may coexist, and each may respond individually to environmental change. Although science's interest lies mainly in the ecology and population dynamics of a single or a few species, one species cannot exempt itself from a network of interactions among all species that are present. Consequently, the grasshopper community becomes a central focus in any rational integrated pest management (IPM) project.

Communities are significantly more complex to evaluate and study than single-species populations. Manipulating one small component of the community network (e.g., of one or a few species) may not evoke the desired, long-term control objectives. Consideration of only one or a few species may lead to unnecessarily short-term solutions or even to unexpected problems. Besides problems associated with community complexity, species assemblages vary greatly from year to year at the same site and vary even more dramatically among sites. Scientists require descriptive and analytical methodologies to clearly devise and assess community management practices. Scientists also must simplify the scope of the problem without sacrificing important connections that prescribe creative solutions.

In this section, I summarize simple, standard approaches and methodologies for describing communities and for assessing the importance of key interactions. Some of these methods are best for sporadic evaluation of random sites on a hit-or-miss basis. Others are designed for developing long-term understanding at sites that are regularly monitored for potential grasshopper problems. Government agencies and private organizations that manage the same large tract over many years can expect to develop comprehensive, community-based IPM programs. But individual ranchers with only intermittent grasshopper problems and few resources cannot. As a result, managers must select which of the following approaches to community evaluation meets their situation. Complete annual censuses and evaluations of environmental conditions are the cornerstones of community studies. These require significant effort, and that cost–benefit ratios ultimately determine the value of studying community relationships.

As I list accepted methods to evaluate grasshopper communities, I will stress the difference between merely describing community composition (species identities) and understanding mechanisms driving species interactions and coexistence. IPM measures interrupt dynamic, often subtle, ecological interactions within and among species. Until we work out the impact of these key interactions for many species combinations in detail, species lists alone provide little insight into future system dynamics surrounding IPM efforts.

Community Descriptions: List of Grasshopper Species Present

A list of grasshopper species is the simplest description of a community and is required in any community-level assessment. A good description includes the relative abundance and absolute density of individual species in a community. Density is important because the number of individuals that are available to interact determines, at least in part, what really happens.

Based on past studies, experts can sometimes develop insights regarding community dynamics from such lists—if certain conditions and species are present. Shifts in species composition among years or among sites suggest that different grasshopper species react differently to changing environments. Such variation in the response to different environmental conditions indicates that either the community shifts from one state to another or that the internal dynamic interactions among species shift. Consequently, the same IPM management practice employed under different conditions may produce different long-term responses depending on the state of the community.

Sampling efficiency can vary with habitat type and its three-dimensional structure as well as overall grasshopper densities. Typical methods include sweeping some predetermined number of times or counting grasshoppers at stationary sample sites (e.g., the "ring technique" of Onsager and Henry 1977, Thompson 1987). Berry et al. review appropriate sampling methods and their justification in chapter VI.10 of this handbook. Remember, in obtaining lists of species' relative abundances, the accurate sampling of rare species is the biggest problem. More samples will reduce the chance of missing rare species. To estimate a sampling intensity that will detect most of these species at your site, plot the cumulative number of grasshopper species collected against some measure of sample intensity (number of individuals collected, number of sweeps, number of rings examined, number of transects, area sampled, and number of habitat types sampled). Figure VII.13–1 illustrates a reasonable sampling schedule. In designing sampling plans, be aware that you will probably encounter some unrecorded species if new habitat types are included. Because of this, plan to sample all habitat types found in the area in the proportion that they occur in the environment.

What rules-of-thumb emerge from species lists? Many species thrive only in areas with open bare areas (e.g., *Ageneotettix deorum).* Other species (e.g., *Paropomala wyomingensis)* require significant vertical structure such as that provided by bunchgrasses. Still other species (e.g., *Melanoplus sanguinipes)* occupy a variety of microhabitats, so that little insight can be gained just by knowing what microhabitats exist at a site. Similarly, even among grasshopper species that eat many plants, the range of readily consumed plant species will be similar among sites. Based on use of both food plants (Joern 1979a, 1983) and microhabitat resources (Joern 1982), community level patterns emerge that may help a manager make decisions (Joern 1979a,b, 1986a). The usefulness of such an approach for developing sound grasshopper IPM tactics is idiosyncratic and case-specific at this time.

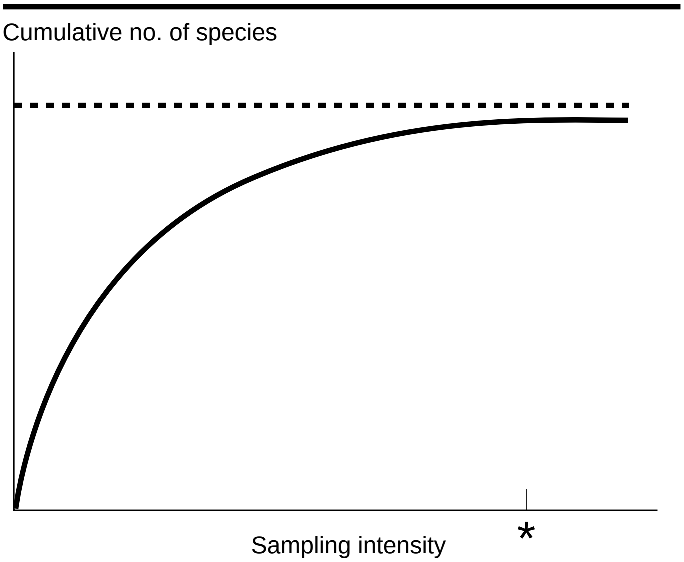

Figure VII.13–1—The number of species sampled is dependent on the sampling intensity. To obtain a good estimate of the number of species at a site, sampling intensity should equal that indicated with an asterisk, near the asymptote for the entire assemblage. If sampling intensity is less than this point, many rare species will likely be missed.

Using Statistics To Estimate Species Replacements and Community Associations

Species replacements and community associations along environmental gradients can be identified using standard multivariate statistical techniques (e.g., discriminant function analysis, principle components analysis, detrended correspondence analysis) or some combination of the statistical techniques developed for ordinating communities (Gauch 1982). As a technique, ordination simplifies multiple species associations by representing the relationships in fewer dimensions using mutivariate descriptive statistics. By using these techniques, you can identify the combinations of species that tend to occur together (and their relative abundances) in association with key attributes of the environment such as vegetation type or soil moisture (fig. VII.13–2). Such community analyses allow you to simplify the community associations along a spatially varying environmental gradient. Be aware of the correlational nature of these results from these analyses. The patterns that you uncover will fully depend on what you include in your initial sampling design. If you add species or sites with different combinations, the ultimate patterns may shift. Ordination provides a refined fit between grasshopper community composition and some environmental gradient, but *you cannot identify dynamic and causal relationships between the two features by using this approach.*

Plotting Against an Environmental Gradient.—You can readily visualize species replacements along gradients by plotting the change in the abundance (or relative abundance) of each species along some environmental gradient (fig VII.13-2a). In this hypothetical analysis, I assess a series of independent sample sites as in number 1 above (a list of grasshopper species). Then, on a species-by-species basis, I plot the abundances (or relative abundances) along the gradient. By comparing these plots among species, you can identify possible environmental conditions at your site best suited and worst suited for each species. In addition, you can compare responses of multiple species along the same gradient.

Multivariate Ordination Techniques.—Species associations can be identified using standard, multivariate ordination techniques (fig. VII.13-2b). While these techniques typically require commercially prepared computer software, the analyses are readily accessible, even on laptop computers. Standard references exist to help the user understand both the statistical guts of the analysis as well as providing insights to interpreting results (Cornell Ecology Programs discussed in Gauch 1982). The computer algorithms help put boundaries around species combinations from each location, largely based on changes in relative abundances rather than in response to massive replacement of individual species. Remember, these boundaries of species composition represent "probability boundaries" and much overlap typically exists in grasshopper species composition among adjoining communities or even when comparing sites some distance away. As a warning: many users of this technology tend to become typological in describing communities and often confuse pattern with a dynamic process. For example, I foresee some managers ordinating grasshoppers from a group of sites and then prescribing specific management options for those assemblages in group A versus group B or C and so on. The assumption that all

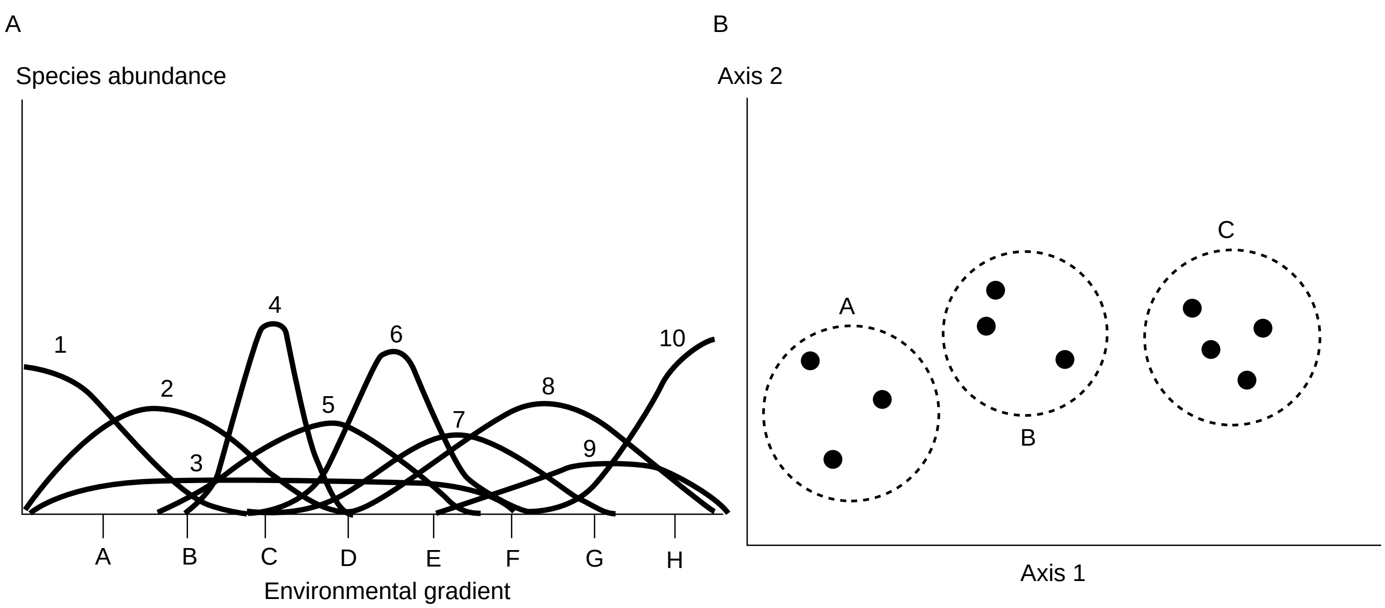

Figure VII.13–2—*A:* Hypothetical distribution of species along some environmental gradient based on sampling at 8 sites (A–H) along a transect. Each curve indicates the distribution along this gradient for a hypothetical grasshopper or plant species. For example, species 4 does best at site C but does not exist at site E while species 3 does not do particularly well at any site but is found along the entire gradient. *B:* This multivariate distribution can be "boiled down" into a simpler relationship using ordination techniques following those outlined in Gauch (1982). Each of these new axes (1 and 2) represent a composite of multivariate data. The points indicated in B represent the average position for each species indicated in A for the two multivariate resource axes developed from a composite of environmental variables. The groupings of species indicated by the dashed lines suggest species that react to environmental conditions in the same fashion. Examples of gradient analyses of grasshopper species along a topographic gradient in Montana are presented in Kemp et al. (1990) and Kemp and O'Neill (1990).

sites exhibiting type A species associations also categorically exhibit the same underlying dynamics is unfounded.

Unless a conceptual framework exists that predicts unique, species-specific relationships, the results will not explain why specific patterns emerge. For example, grasshopper species assemblages often change predictably as the species composition of the plant community changes (see chapter IV.3). What dynamic relationship exists between the two components of this analysis to explain the results? Unfortunately, insufficient information exists to tease apart such relationships, even if the pattern is very strong. Sometimes specific theories exist that predict particular species responses in abundance or in association with specific habitats. In these situations, additional insights regarding dynamic, causal mechanisms might emerge from pattern analysis, but this notion still requires experimental testing to uncover the underlying reasons for the relationships fully. Scientists must base management options on *processes* driving community dynamics, not on easily measured patterns. This fact is unfortunate because scientists can more readily establish measures of pattern than uncover the underlying dynamic mechanisms.

Using Controlled Manipulations To Uncover Site-Specific Dynamics

Experimental manipulation of species interactions can provide powerful community level insights into the dynamic forces that organize communities. However, the effort is great. From an IPM framework, subtle shifts in species composition that changes in the underlying interaction dynamics may provide the key for developing the correct management strategy. After all, those IPM practices that work in concert with naturally occurring dynamic processes will most likely lead to long-term success. However, uncovering the specific nature and strength of interactions among species, including their impact on resulting population densities and community structure, will require experimental manipulations under field conditions. Standard experiments that might uncover these relationships are time consuming and complex.

Consequently, an efficient experimental approach requires a strong conceptual framework so that science can simultaneously evaluate key competing possibilities and that investigators can reject alternatives based on experimental results. The conceptual framework identifies alternate hypotheses. By simultaneously testing competing explanations of community pattern and process through experimentation, the manager can rapidly narrow the options. Then it becomes possible to uncover the best explanations upon which to base management options. Despite the difficulties and cost, I strongly believe that the intense effort required to uncover site-specific dynamics using controlled manipulations will pay off, in the long term, for grasshopper IPM managers. Examples of sites that should profit from intensive studies include public lands and large private holdings with constant or predictable land-use practices and a history of grasshopper problems. If managers feel insecure about performing all of the above work by themselves, they should allocate some management funds to contract for research by competent scientists.

A current example illustrates the above process. A conceptual framework that defines alternate views of the problem, combined with experimental manipulation and coupled with appropriate comparisons and descriptive analyses, allows recognition and interpretation of the dynamic interactions that regulate community-level processes. As a general framework, the alternatives include “top-down” versus “bottom-up” processes (Hunter et al. 1992). As herbivores, grasshoppers occupy an intermediate trophic (nutrition) position in the food web, with food plants below them and natural enemies (e.g., parasitoids, invertebrate and vertebrate predators, or fungal, bacterial, or viral pathogens) positioned above them.

What major forces limit grasshopper populations in this food web? From a control standpoint, this information provides the clue to appropriate management planning. Bottom-up forces can arise from insufficient nutrients either when grasshoppers compete for limited food or when time constraints interfere with feeding and digestive capability. Top-down forces can arise from the actions of natural enemies. Other chapters of the Grasshopper Integrated Pest Management User Handbook provide detailed examples of each type of interaction.

Descriptive studies cannot untangle this set of potential interactions, but manipulative experiments can. In fact, under natural conditions, bottom-up (Belovsky and Slade 1995) and top-down (Joern 1986b, 1992) forces operate simultaneously, and either one can drive the interactions and can thus determine the final densities of coexisting grasshoppers (Belovsky and Joern 1995). More importantly, reciprocal indirect effects of species on each other can potentially be more important than the direct interactions. Scientists can see such responses only through experimentation.

The Role of Experimentation in Developing "True" IPM for Grasshoppers

True IPM will require successful description of the above relationships in its development, and perhaps will lead to the development of "ecotechnology" based on a firm conceptual foundation. For example, here are the types of questions that we must address experimentally: How do grasshoppers compete for scarce food resources? Which species are the best competitors for the available food supply? What impacts do such interactions exert on the resulting grasshopper community structure? Will the food resource base change as environmental conditions change and with what consequences? Are competitive interactions altered in response to changing food supplies? How important are natural enemies in deciding which grasshopper species survive and in what relative abundance? How do competition and predation interact to affect grasshopper communities? How do abiotic (weather) and biotic (species-interaction) features of the environment interact to affect grasshopper communities, if they exert any influence at all? Results from experiments to answer these and related questions will allow land managers to define explicitly the key interactions that describe the community relationships a particular grasshopper infestation. Managers can then identify links that will provide the desired IPM results, or those that are susceptible to disruption and will lead to unwanted and unintended results.

Final Comments

Grasshopper IPM must focus on entire grasshopper assemblages, even if only a small proportion of the species are economic targets. Interactions among species may lead to unexpected consequences from control efforts if we ignore rare but otherwise functionally important taxa. Both species lists and more complicated statistical descriptive techniques of grasshopper communities will provide some guidelines, but neither will provide direct insights about dynamic relationships. Because effective control will result in permanent or at least long-lasting alteration of species interactions, scientists would like to understand the dynamics of these interactions. Frankly, much work remains before this approach bears fruit. However, the rich conceptual framework that underlies community dynamics suggests that many important insights will emerge and hopefully will revitalize the basis of control and management planning.

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