

# Generality in ecology: testing North American grassland rules in South African savannas

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Ecology has emerged as a global science, and there is a pressing need to identify ecological rules – general principles that will improve its predictive capability for scientists and its usefulness for managers and policy makers. Ideally, the generality and limits of these ecological rules should be assessed using extensive, coordinated experiments that ensure consistency in design and comparability of data. To improve the design of these large-scale efforts, existing data should be used to test prospective ecological rules and to identify their limits and contingencies. As an example of this approach, we describe prospective rules for grassland responses to fire and rainfall gradients, identified from long-term studies of North American grasslands and tested with existing data from long-term experiments in South African savanna grasslands. Analyses indicated consistent effects of fire on the abundance of the dominant (grasses) and subdominant (forbs) flora on both continents, but no common response of grass or forb abundance across a rainfall gradient. Such analyses can inform future research designs to refine and more explicitly test ecological rules.

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Progress in ecology has resulted from testing specific predictions derived from hypotheses (the hypothetico-deductive model) and through the synthesis of accumulated results into general patterns and underlying mechanisms (Pickett *et al.* 1994). The ultimate goal for ecology, like all sciences, is the refinement of knowledge into theories and laws that are predictive and able to

withstand repeated tests (Murray 2001). In laboratory-based sciences, the ability to precisely and independently repeat experiments, a key step in the scientific method, is facilitated by the rigorous control of experimental conditions. In ecological experiments, particularly those conducted in the field, the background environment is always changing; genetic composition and variability among the study organisms are seldom constant, and both organism behaviors and ecosystem states are derived from an often unknown past. All of these factors reduce the likelihood that repeated experiments will yield similar results. An unfortunate outcome is the perception that ecological systems are idiosyncratic and have limited predictability.

Two comments from the literature illustrate the inherent challenges of ecological studies. Over 20 years ago, while conducting experiments in the field, plant ecophysiologist Melvin T Tyree (1983) noted that “progress was rather slow because weather conditions could not be arranged to meet experimental requirements”. Later CAS Hall (1988) lamented that “if physicists had to model electrons that behaved differently when they were hungry, they would probably be not much ahead of ecologists...”.

Such challenges are perhaps responsible for the restrained pace of synthesis, the combining of results from numerous studies into coherent generalities, and consequently the slow development of widely accepted laws in ecology. Indeed, the existence and generality of laws for ecological systems has long been debated (McIntosh 1985; Lawton 1999; Berryman 2003; Colyvan and Ginzburg 2003), and some have argued that it is fruitless to seek laws because of the complexity of these systems (McIntosh 1985; Peters 1991). To some extent, this debate reflects different definitions and expectations of sci-

## In a nutshell:

- Proposing ecological rules and testing their limits is necessary for ecology to become a more predictive science
- Rules enabling forecasts of community and ecosystem responses to key drivers would be valuable to managers and policy makers
- Prospective rules that predict responses to fire frequency and rainfall gradients, based on long-term studies in North American grasslands, were tested in South African savanna grasslands, using existing data from ongoing, long-term experiments
- Analyses indicated consistent effects of fire on the abundance of grasses and forbs in both grasslands and savannas, but not consistent responses of forbs to rainfall gradients
- Synthetic analyses of existing data can provide insight into the general applicability of proposed rules, identify contingencies and data needs, and guide future research

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**Figure 1.** Intensive study of ecosystems and experimental manipulation of the drivers that structure them can lead to the formation of rules that have predictive value at hierarchical levels ranging from the organism to the ecosystem. For example, the long-term study of fire on experimental watersheds at the Konza Prairie LTER site has led to a series of predictive rules for this mesic grassland (Knapp *et al.* 1998), but the generality of these rules is unknown. Determining how well rules apply in other systems and identifying those contingencies or exceptions that lead to alternative responses is an important step towards ecology becoming a more predictive science.

entists. Scientific laws can be defined as conditional statements of relationship or causation, or as statements of process that always hold within defined limits (Pickett *et al.* 1994). Because this definition suggests that laws are immutable, it may be too restrictive for many ecological systems. We suggest an important, albeit subtle, distinction, namely that ecologists seek rules rather than laws. Rules still reflect the notion of generality and conditional probability, but they place less restrictive boundaries on expectations (Lawton 1999). Rules, after all, are made to be broken.

Most ecologists would agree that ecological rules exist, at least as defined by Lawton (1999) as “general principles that underpin and create patterns”, and ecologists have certainly made progress in testing general ecological processes and phenomena in multiple ecosystems (eg Pickett and White 1985; Brown *et al.* 2001; Loreau *et al.* 2001; Rees *et al.* 2001; Enquist *et al.* 2003). However, despite a wealth of comparative studies, ecological rules and their predictive limits are seldom explicitly examined (Figure 1). This may be because ecologists are wary of the uncertainties associated with field experiments and they know, as Lawton cautioned, that some level of contingency (exceptions related to history or other events) must almost always temper them. Nonetheless, distilling generalizations from an ever-increasing body of detailed ecological data, formulating prospective rules that govern ecological systems, and explicitly testing them are essential steps for making ecology a more predictive science (Figure 2).

Only a few ecological rules have been formally proposed that apply to both multiple taxa and systems (eg Rosenzweig 1995; Ritchie and Olff 1999; Reynolds 2002; Turchin 2001; Enquist *et al.* 2003; Berryman 2003). Some of these span orders of magnitude in scale, and are products of the emerging field of macroecology (Brown 1995). Despite their promise, such rules are often questioned on a variety of grounds (ie Murray 2001; Coomes *et al.* 2003; Harte 2004; Cyr and Walker 2004). Indeed, Simberloff (2004) recently conceded that the discipline of community ecology has no general rules in the sense that physics does, but instead has only “fuzzy generalizations”. He suggested, as did Lawton, that this occurs in part because the basic units of community ecology – species – are more numerous, diverse, and complex than the basic particles of physics. Thus, ecological rules may need to focus on a different set of ecological units, such as metabolic pathways, functional traits, or biomass. In this regard, we concur with Cooper’s (1998) arguments that there are many potential ecological rules (causal, theoretical, and phenomenological) that may have strong

predictive capabilities, when their boundaries or limits are correctly identified. This perspective is consistent with a broader definition of ecological rules, modified from Lincoln *et al.* (1990), as generalizations or statements that predict the occurrence of a particular ecological phenomenon, if certain conditions are met. Thus, rules describe how ecological systems will behave within certain boundaries (Berryman 2003), and allow for predictions within these constraints. Indeed, general rules pertaining to the ways in which terrestrial ecosystems recover from disturbances were proposed long ago (Odum 1969), though many are yet to be formally tested.

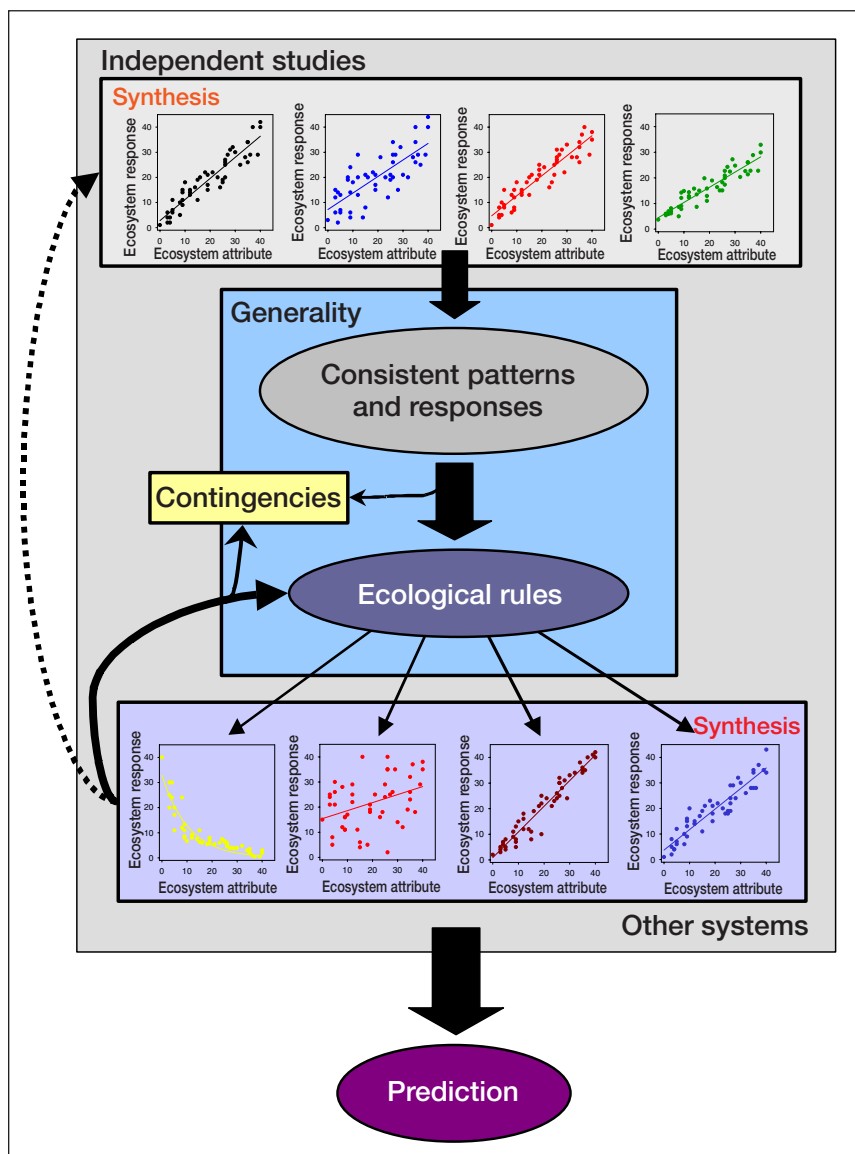
Generalizations that could be applied to ecological patterns and processes, and their underpinning rules, based on the key factors that drive and constrain communities and ecosystems, would certainly be valuable in forecasting the responses of biomes to global change (Dynesius *et al.* 2004). They would also help land managers and policy makers, who are grappling with resource and conservation issues in a rapidly changing world. The most robust rules – either empirically or theoretically derived – should be able to withstand the test of time, and will therefore probably be generated from the long-term study of ecological systems (eg the Hubbard Brook Experimental Forest; Bormann and Likens 1979; Figure 1). However, for ecological science to advance, it is critical to test predictions from rules in systems other than those used to develop them. Clearly, if the drivers responsible for the structure and dynamics of particular ecosystems have been correctly identified and are

mechanistically understood, ecological rules should have predictive value in other, similar systems. Testing rules in other ecosystems provides a means of assessing their generality, as well as detecting important contingent factors (Dynesius *et al.* 2004; Figure 2).

How might an assessment of general ecological responses, their underpinning ecological rules, and their contingencies, best be accomplished? Currently, there are two general methods. The first is the standard comparative approach (eg Grime 2001), in which observations and mechanistic experiments designed to elucidate key traits of organisms or ecosystem drivers can be used to generate prospective rules and test predictions derived from them. The preferred approach for identifying general responses, formulating rules, and testing them includes coordinated experiments designed for synthesis prior to initiating the research (Hector *et al.* 1999; Webster *et al.* 2003). This “*a priori*” approach ensures consistency in the implementation of treatments, and commonality in the way data are collected. However, the relevant time scales for the manifestation of many ecological processes and patterns can exceed 5–10 years (Callahan 1984; Brown *et al.* 2001), making such experiments expensive and their outcomes less than timely.

An alternative to an *a priori* approach is *post hoc* (after the fact) synthesis, which involves combining existing results from a collective body of research designed to elucidate specific ecological processes or phenomena. Traditional literature reviews are qualitative examples of this type of approach. More recently, meta-analyses of results from studies that focus on a specific manipulation (such as responses to elevated CO<sub>2</sub>; Jablonski *et al.* 2002) or specific ecological relationships (Waide *et al.* 1999) have permitted more quantitative analyses. Formal rules can be created and their limits tested with either *post hoc* or *a priori* approaches (Figure 2).

An additional and complementary *post hoc* approach involves the analysis and synthesis of raw data, rather than results, from past studies. What distinguishes this kind of approach is that data can be used from studies that were not necessarily focused on similar ecological questions. Previous analyses may not even be of interest – a fundamental departure from traditional literature



**Figure 2.** Framework describing the iterative process of formulating ecological rules. The syntheses of research results from independent studies (top) may be planned *a priori* from coordinated research programs or result from the *post hoc* analysis of disparate studies. After consistencies in pattern and process are idealized, with potential contingent factors noted, these prospective rules can be explicitly tested in other systems. This may be accomplished with new research or through the continued analysis and synthesis of existing data and results. Through the synthesis of these assessments (dotted line), formal ecological rules can be articulated and predictions become more robust. Throughout the process, the identification of contingent factors will modify and ultimately define the predictive limits (ie the domain) of these rules. Contingent factors themselves can also serve as foci for additional research, further advancing ecological understanding.

reviews and meta-analyses. Instead, formerly disparate datasets are combined and made comparable, so that new questions can be addressed. In this way, we can take advantage of the abundant data that currently exist, not to mine them for patterns (Burnham and Anderson 2002), but rather to test new predictions. This approach also avoids the publication and investigator bias that plagues meta-analyses (Tomkins and Kotiaho 2004). Of course



### Panel 1. Comparison of key attributes of *a priori* (planned) synthesis of ecological data versus *post hoc* (after the fact) synthesis of existing data from disparate studies

Identifying general ecological patterns and processes, and their underpinning rules, is best accomplished through synthesis planned initially as part of the study. However, *post hoc* synthesis of data has several advantages, including low cost and timeliness; results can also be valuable in guiding new research.

#### Attributes of *a priori* synthesis:

- (1) Experiments are motivated by common questions/hypotheses, with only minor subsequent modifications. Final synthetic analyses explicitly address these questions
- (2) Core experiments/studies share a common design and sites are selected to maximize the usefulness and generality of results
- (3) Rare or unplanned events during the course of study often improve understanding because of the common experimental design and structure
- (4) Datasets are collected consistently and are comparable temporally and spatially
- (5) Context (spatial and temporal) for interpretation is predetermined and remains consistent
- (6) Cost is substantial, particularly if long-term data are needed – includes data collection and synthetic analyses

#### Attributes of *post hoc* synthesis:

- (1) Questions/hypotheses are exploratory and will probably be altered substantially, depending on data availability and quality
- (2) Experiments/studies are variable in their design and study sites can be diverse
- (3) Unusual events inevitably affect some studies but not others and thus add uncertainty
- (4) Data are variable in quality and temporal and spatial dimensions and units
- (5) Context for interpretation will probably decrease (spatially and temporally) as data limitations are identified
- (6) Cost is minimal – limited to synthetic analyses

there are limitations to this, and any *post hoc* approach, but new analyses of data can provide substantial ecological insight, generate new hypotheses, and improve future experiments, particularly if these data were collected over long time periods.

### ■ *A priori* versus *post hoc* synthesis

Through experience with both *a priori* and *post hoc* syntheses of ecological data we have identified important strengths and weaknesses for each approach (Panel 1). Two brief examples of each type of synthesis are provided, each using results from long-term ecological research (LTER) sites to illustrate the differences. We focus on examples based on long-term studies because this is where *post hoc* synthesis has the greatest value, when compared to the initiation of new research. We then propose basic rules for ecosystem structure derived from studies of temperate grasslands in North America and test them in South African sub-tropical savanna grasslands.

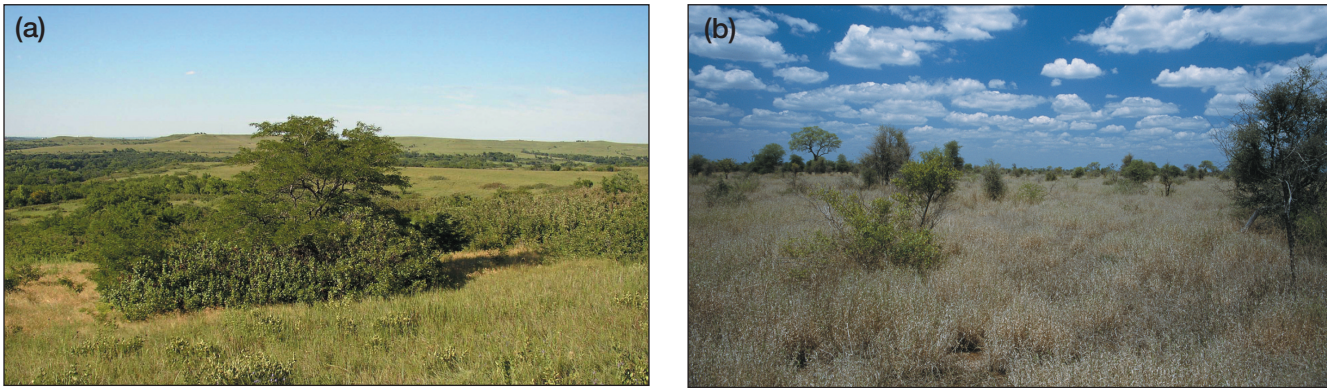
LTER sites are excellent examples of research programs designed for synthetic analyses and the development of ecological rules for specific biomes because of the breadth of data collected from the level of the individual organism to the entire ecosystem, and because all programs have a unifying, site-based perspective (Callahan 1984). At the Konza Prairie LTER site, a mesic grassland in northeastern Kansas, long-term manipulations of key drivers (fire and grazing)

are maintained across replicate watersheds to address a number of questions regarding ecological patterns and processes in grasslands (Knapp *et al.* 1998; Figure 1). Consistent with the LTER paradigm, numerous response variables are measured spatially across treatment and landscape gradients and temporally across years in which the climate varies naturally. Small-scale plot studies and short-term experiments complement long-term studies to elucidate specific ecological interactions.

Based on data from several of these studies, Collins *et al.* (1998) assessed the interactive roles of fire and large herbivores in determining the productivity and community composition of the Kansas site. They showed that the cumulative effects of frequent fire – increased productivity and biomass of the dominant grasses, but reduced plant species richness – were mediated by grazing. Large herbivores enhanced plant species richness in frequently burned areas

through reductions in the biomass of the dominant grasses. A mechanistic link to grass canopy (biomass) removal was made possible by combining results from complementary plot-level mowing experiments, in which similar response variables were measured (Collins *et al.* 1998). Combining data from distinct fire, grazing, and mowing experiments to understand controls on community composition was made possible by an experimental design that facilitated a *priori* synthesis of results (Panel 1).

The LTER program also provides an example of *post hoc* synthetic analyses (Knapp and Smith 2001). In this case, aboveground net primary production (ANPP) data, collected for a variety of different site-specific purposes at all LTER sites, were combined to test hypotheses about continental-scale patterns and controls of ANPP, and inter-annual variability in productivity. Due to differences in the quality and temporal extent of ANPP data collected between sites, the original questions were revised and the context and scope of the analysis was altered. As a result, just a subset of the data was used. Similar alteration in scope as a result of data limitations is common in *post hoc* analyses (Panel 1). Nonetheless, *post hoc* analyses of these data proved valuable, indicating that although mean annual rainfall was strongly related to mean ANPP across sites, inter-annual variability in rainfall was not related to temporal variability in ANPP. Instead, a more complex model that included the ability of producers to respond to variation in resources was developed to explain these patterns.



**Figure 3.** (a) Upland view of an experimental watershed on the Konza Prairie Biological Station in northeastern Kansas. Konza Prairie was one of the original six LTER sites and is dominated by  $C_4$  grasses; the abundance of  $C_3$  woody species is dependent on fire frequency (Knapp *et al.* 1998). (b) View of an experimental burn plot (EBP) near Satara, Kruger National Park, South Africa. This 7-ha plot, part of an experiment ongoing for > 50 years, is frequently burned and is also dominated by  $C_4$  grasses, with widely dispersed  $C_3$  shrubs and trees.

In both examples, new understanding of ecological patterns and processes emerged from synthetic analyses of data. However, the process of understanding differed. Although *a priori* synthesis most closely resembles a traditional scientific approach and *post hoc* synthesis clearly has greater limitations, using existing data in such analyses adds value to both completed and ongoing studies, and may be valuable in identifying knowledge and data gaps.

### ■ Searching for ecological generality in grasslands and savannas

Results from either *a priori* or *post hoc* syntheses can directly lead to the generation of ecological rules. However, a key step towards increasing predictability in ecology is to apply rules derived from one system to another (Figure 2). The goal is to generate a broader understanding of each system, and also of general ecological rules. If the rules apply across systems, we can hypothesize that mechanisms driving patterns in one system operate similarly in others, and we can then design experiments to test this hypothesis. If the rules do not apply, we can investigate which assumptions in one system are violated in the other, or in other words, identify

important contingencies. In either case, new knowledge and understanding are derived about each system, research decisions can be prioritized, new cross-site experiments can be initiated, and the process of synthesis can begin anew.

To illustrate this process and the *post hoc* synthesis of data rather than results, we summarize our experiences from a recent working group held at the National Center for Ecological Analysis and Synthesis (Santa Barbara, CA), in which long-term data were analyzed to test three proposed ecological rules concerning key drivers (fire, grazing, and moisture availability) of grassland plant community structure (Panel 2). These rules are based on well-known patterns and responses observed in North American grasslands. The long-term datasets analyzed to generate them were from grassland LTER sites in Kansas and New Mexico. To test the generality of the rules in a savanna grassland ecosystem, we used data from a long-term (over 50 year) fire experiment (Biggs *et al.* 2003) in Kruger National Park (KNP) in the Republic of South Africa, and two long-term monitoring programs in, and adjacent to, the KNP (Table 1; Figure 3). The savanna grasslands of South Africa share many attributes with these North American grasslands:  $C_4$  graminoid dominance, common or co-

**Table 1. Description and locations of long-term studies included in analyses of fire, grazing, and precipitation drivers in the savanna grasslands of North America (NA) and South Africa (SA)**

Site	Location	PPT	Biome type	Treatments	Dates of data	# plots	Published description
Konza LTER	Kansas, NA	834	Mesic grassland, temperate	Experimental fire, grazing	1984–2000	660	Collins 1992
Sevilleta LTER	New Mexico NA	250	Xeric grassland, temperate	Experimental grazing	1989–2002	Transects (400 m)	Ryerson and Parmenter 2001
Experimental burn plots	KNP, SA	495, 551, 653	Savanna, subtropical	Experimental fire, natural grazing	1998, 2001	32	Biggs <i>et al.</i> 2003
Veld Condition Analysis	KNP, SA	499 (465–700)	Savanna, subtropical	Natural fire and grazing	1989–1999	533	Kennedy <i>et al.</i> 2003
Game reserves	Adjacent to KNP, SA	547 (411–690)	Savanna, subtropical	Managed fire, grazing	1989–2001	544	Peel <i>et al.</i> 2004

KNP = Kruger National Park; PPT = annual precipitation (in mm; multiple values or ranges provided when plots were arrayed over large areas).

### Panel 2. General grassland responses in plant community structure to fire, grazing, and moisture availability

Responses were synthesized from North American studies conducted over the past 50 years. These can be viewed as prospective ecological rules to be tested in South African savannas, as well as other grasslands. Prospective rules one and two are based primarily on Konza Prairie LTER *a priori* studies. Rule three is based on historic observations and studies, as well as current research at the Konza Prairie and Sevilleta LTER sites.

(1) In mesic grasslands with no large ungulate grazers, frequent fire enhances dominance by graminoids and reduces relative forb abundance. This results in reduced plant community richness (Collins 1992).

(2) Grazing by large ungulates reduces graminoid dominance in mesic grasslands, and this offsets the effect of frequent fire on plant community richness (Collins *et al.* 1998; Knapp *et al.* 1999).

(3) The relative abundance of forbs increases in grasslands from xeric to mesic sites, but large ungulate grazers temper this pattern (Weaver 1954; Risser *et al.* 1981).

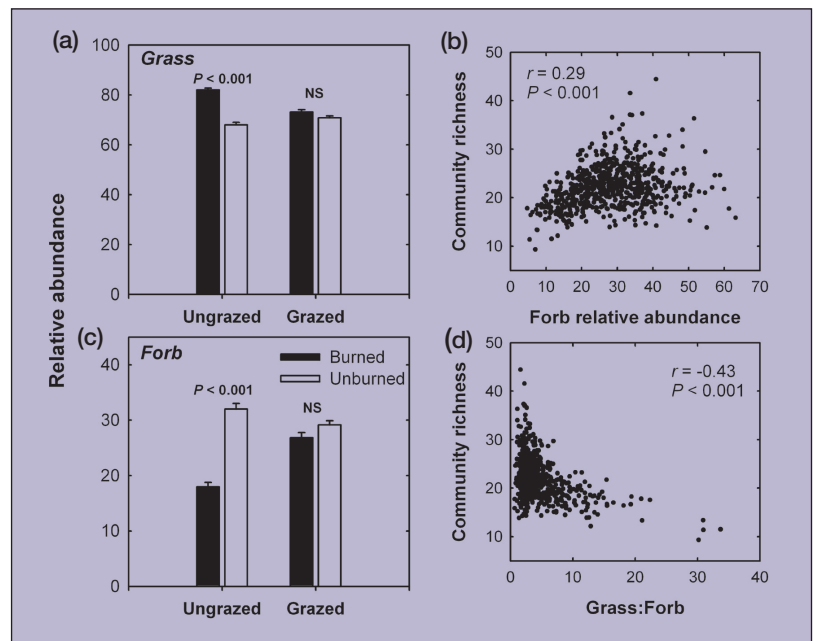
dominant C<sub>3</sub> woody plants, fire, grazing by large herbivores and extreme climatic variability (drought) as key drivers of ecosystem structure and function (Scholes and Walker 1993; Bond *et al.* 2003). It is important to note that these long-term studies in South Africa were not designed to elucidate a specific ecological phenomenon, nor were they intended for broad comparative analyses. Rather, they were designed to focus on local management issues (Biggs *et al.* 2003).

We assembled datasets from these five long-term studies and compiled key data attributes (temporal, spatial, taxonomic resolution of sampling). This process allowed us to identify a common basis from which analysis could proceed. Initial barriers to synthesis included differences in taxonomic resolution of the datasets. Although all plant species were identified in North American studies, most of the South African sampling was less detailed. For example, as the resource of interest from a management perspective, only the grass and tree species were identified and the remaining species were categorized by growth form (graminoids, forbs, and, in some cases, smaller woody plants). Size of plots and sampling methodology also varied. Analysis of community richness was therefore not possible. Instead, all data had to be transformed to a common response variable that could still be related to plant community richness or diversity. In this case, we used relative grass and forb abundance. A third barrier involved key differences in the ways in which fire and grazing occurred at each site. At Konza Prairie, fire was imposed at fixed intervals and grazing treatments occurred independently, so

that their effects could be assessed in a full factorial design. In contrast, in the South African studies, fire was imposed by natural, prescribed, and experimental means at various intervals, and grazers were present at all times. This did not allow for the separation of fire and grazing effects, but only for their combined effect at high versus low fire frequency.

After the North American data were transformed from species-level resolution to growth form categories to reflect attributes of the South African data, the patterns and the prospective rules were reassessed to ensure that they were still supported by the North American grassland datasets. This also allowed us to determine the amount of information lost due to data transformation. Converting data from species-level resolution to growth form categories did not alter predictions regarding the impact of fire and grazing on grass dominance and forb abundance at the Konza LTER site (Figure 4). Moreover, growth form abundance was significantly related to community richness (Figure 4), suggesting that this taxonomically coarse metric has predictive power for the emergent property of diversity. Thus, little information was lost by focusing on growth form abundance, and the link between key drivers (fire and herbivory) and community richness was maintained.

Because of differences in the imposed fire regimes at the North American and South African sites, and the presence of herbivores at all savanna sites, only high (fire



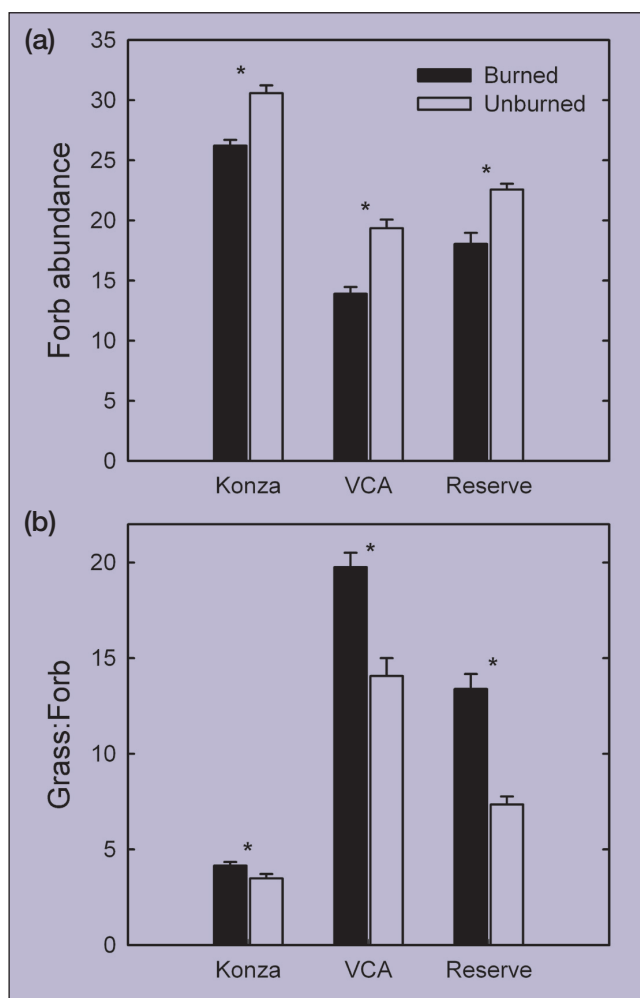
**Figure 4.** (a and c) Effect of long-term (>15 years) frequent burning (annual spring fire) versus protection from fire (unburned) on the relative abundance of graminoids (primarily C<sub>4</sub> grasses) and forbs (C<sub>3</sub> dicots) in mesic grassland at the Konza Prairie LTER site. Sites were either grazed by native herbivores (*Bos bison*) or protected from these grazers. (b and d) Relationship between plant community species richness and forb abundance, or the ratio of grass:forb abundance across all fire and grazing treatments. Statistical significance is indicated in each panel; NS = not significant.



every 1 or 2 years) versus low fire frequency categories in the presence of grazers could be assessed. Re-analysis of Konza LTER data with these fire frequencies as a main effect indicated that frequent fire led to reductions in forb abundance, regardless of ungulate presence (Figure 5). The influence of grazing could therefore be removed from the first rule (Panel 2). When the South African datasets were analyzed, similar patterns emerged, indicating that the effects of fire were consistent in grassland and savanna ecosystems across broad ranges of grazing intensity and types of large ungulates (Figure 5). Although frequent fire enhanced graminoid dominance and reduced forb abundance in both systems, it is important to note that the link between forb abundance and community diversity evident in North American grasslands remains to be evaluated in South African savannas (Fynn *et al.* 2004; Uys *et al.* 2004).

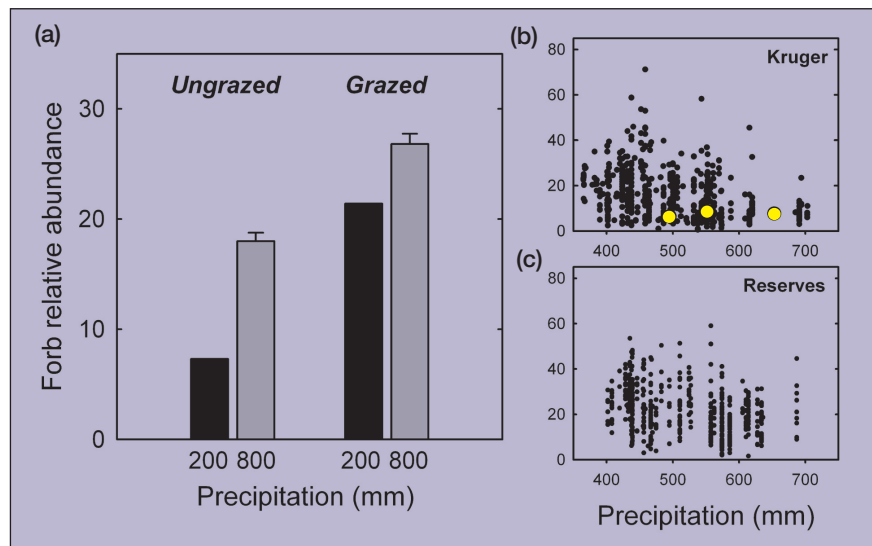
When contrasting xeric and mesic LTER grassland sites in North America, a positive relationship between forb abundance and precipitation has been described in the literature (Weaver 1954; Panel 2) and this pattern is observed today (Figure 6). In contrast to the strong support for a consistent fire effect on grass/forb abundance, such a relationship was not evident in the South African sites (Figure 6). In North America, relative abundance of forbs was more than two-fold higher in mesic (Konza) as opposed to xeric (Sevilleta) grasslands without grazers, each representing the endpoints of a central US grassland precipitation gradient. The addition of large ungulates weakened this relationship, but the pattern was still evident (Figure 6). Across South African sites, no underlying pattern of forb abundance and precipitation was detected. Although the range of precipitation levels was less in South Africa, the lack of even a trend in the relationship between forb abundance and precipitation suggests that this pattern cannot be generalized to subtropical savannas. This may be because South African savannas differ markedly from North American grasslands in large herbivore diversity (much greater in South Africa; McNaughton and Georadiis 1986; du Toit 2003) and evolutionary history (South African savannas are much older; Owen-Smith and Cumming 1993). Either may influence plant community-herbivore relationships. Nonetheless, these results suggest that needed insight could result from manipulating grazers in these savannas in ways comparable to North American grassland studies.

These examples of synthetic analyses of existing data identify additional key considerations of *post hoc* synthesis. These include some drawbacks (eg the need to alter the scope and type of questions being addressed whenever data limitations are identified), but there are benefits. Such activities may spur re-analysis of data and provide new insight. In this case, data from Konza had not been analyzed by growth form to determine if the effect of fire frequency on plant community composition was sufficiently robust



**Figure 5.** (a) Response of forb abundance and (b) the ratio of grass:forb abundance to long-term fire frequency (burned = fires annually or biannually, unburned = fires occurring less than once in 8 years) at a mesic grassland in North America (Konza Prairie) and two savanna grasslands, one in South Africa's Kruger National Park (KNP; VCA = Veld Condition Analysis) and the other adjacent to KNP (Reserve = sites managed as game reserves). Grazing intensity was variable within each site. Standard errors are shown with each bar and statistical significance is indicated by an \*. Data from the experimental burn plots in Kruger could not be included due to inadequate replicates of main treatments.

to be detected regardless of grazing intensity. From a regional perspective, this level of analysis may be particularly valuable, since grazing pressures and fire frequency are quite variable in the Great Plains grasslands. Knowledge of the broad impacts of potential shifts in fire regimes on forb abundance, community richness, and biodiversity in grasslands and savannas has clear conservation implications. Finally, although using data from different studies may not allow for the kind of rigorous, quantitative tests of rules that *a priori* synthesis can offer, qualitative (directional) tests are possible, and these can yield insights and provide direction for future research.



**Figure 6.** (a) Pattern of increasing forb abundance with increasing annual precipitation, as exhibited by the comparison of relative forb abundance at two LTER grassland sites in North America (dark bars = the arid Sevilleta LTER site in New Mexico; gray bars = the mesic Konza Prairie LTER site in Kansas). Also shown is the increase in relative forb abundance with grazing, which tempers the effect of precipitation. (b and c) Lack of a relationship between forb relative abundance and precipitation in savanna grasslands of South Africa, based on data from three long-term studies. Kruger (KNP) data are from the Veld Condition Analysis study (dark circles) and the experimental burning plots study (yellow circles). Reserves data are from sites adjacent to KNP managed as game reserves.

## Conclusions

In the past, the discipline of ecology has been dominated by detailed, short-term studies at a single (local) spatial scale (McIntosh 1985). Most ecological research today is still of short duration and narrowly focused. This occurs despite recognition that our understanding of ecological processes, and how they shape the patterns and dynamics of complex biological systems, can be limited by our failure to consider the effects of history, contingent factors, and regional and global drivers. This, in turn, compromises our ability to generalize across multiple spatial and temporal scales (Lawton 1999; May 1999; Thompson *et al.* 2001). With the global nature of new ecological drivers, such as climate warming and species invasions, and the expectations imposed on policy makers and managers to respond to these environmental challenges, we need to identify general patterns and ecological rules that apply broadly. We also need to test their limits (Figure 2) in order to identify potential contingent factors that result in exceptions to the rules. This is particularly important given that financial resources will never be sufficient to support the study of complex ecological phenomena in all ecosystems worldwide. Clearly, other approaches must be adopted.

Fundamental ecological laws that span multiple taxonomic levels, biomes, or ecological hierarchies, though elusive, should still be sought (Murray 2001; Enquist *et al.* 2003). However, through the careful selection of key ecological attributes or processes, we should accept Lawton's implicit challenge to develop formalized "ecological rules" where possible. Such rules can and should be devel-

oped for grasslands, forests, lakes, and other systems, as tools for improving scientific understanding and natural resource management. Ultimately, ecological rules should be tested with research programs specifically designed for this purpose, but an initial, cost-effective step is to more fully utilize the diverse and numerous datasets available from studies around the world. The Ecological Society of America's *Ecological Archives* is one repository for such data. This information may prove invaluable in the search for generality in ecological patterns and processes and for testing specific predictions in other systems. At a minimum, their synthesis adds value to the original research by prompting novel re-analysis and informing research designs for future studies that include *a priori* synthesis.

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