

## Combining field experiments and individual-based modeling to identify the dynamically relevant organizational scale in a field system

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Community ecologists continually strive to build analytical models that realistically describe long-term dynamics of the systems they study. A key step in this process is identifying which details are relevant for predicting dynamics. Currently, this remains a limiting step in development of analytical theory because experimental field ecology, which provides the key empirical insight, and theoretical ecology, which translates empirical knowledge into analytical theory, remain weakly linked. I illustrate how an individual-based computational model of species interactions is a useful way to bridge the gulf between empirical research and theory development. I built a computational model that reproduced key natural history and biological detail of an old-field interaction web composed of a predator species, a herbivore species and two plant groups that had been the subject of extensive previous field research. I examined, using simulation experiments, how individual behavior of herbivores in response to changing resource and predator abundance scaled to long-term population-level and community-level dynamics. The simulation experiments revealed that the long-term community dynamics could be highly predictable because of two counterintuitive reasons. First, seasonality was a strong forcing variable on the system that removed the possibility of serial dependence in population abundance over time. Second, because of seasonality, short-term behavioral responses of herbivores played a much stronger role in shaping community structure than longer-term processes such as density responses. So, simply knowing the short-term responses of herbivores at the evolutionary ecological level was sufficient to forecast the long-term outcome of experimental manipulations. This study shows that an individual-based model, once it is calibrated to the real-world field system, can provide key insight into the biological detail that analytical models should include to predict long-term dynamics.

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A persistent challenge in community ecology is to develop analytical models that faithfully capture important mechanistic details of natural systems in order to make reliable predictions about community dynamics (McCauley et al. 1990, Rosenzweig 1991, Levin 1992, Werner 1992, Abrams 1995, Peckarsky et al. 1997). A critical first step in model development is resolving which mechanistic details are important for describing

dynamics analytically and which details can be safely abstracted (McCauley et al. 1990, Rosenzweig 1991, Levin 1992, Werner and Anholt 1996).

Theoretical ecology is often handicapped at this stage because resolving which details sufficiently describe dynamics requires a fairly complete empirical understanding of the way species interaction mechanisms are causally linked to long-term dynamics. In practice, this

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insight is difficult to obtain solely from empirical research. Empirical ecology can quickly provide insight into the myriad interaction mechanisms shaping species interactions in a system via short-term field experiments. However, logistical constraints usually prevent the experiments from being conducted long enough to evaluate the linkages between mechanism and long-term dynamics. Field studies that do generate long-term time series data often do not provide the kind of resolution needed to understand which underlying mechanisms are driving the dynamics. When faced with this dilemma, theoretical ecologists are often forced to make educated guesses about which mechanisms to include in their analytical models. This paper illustrates how to reduce some of the guesswork in model development by showing how information from short-term field experiments can be used to identify dynamically relevant mechanisms for models predicting long-term community dynamics.

The approach enlists an individual-based model or IBM (DeAngelis and Gross 1992) as an intermediate step in theory development. The appeal of using an IBM is that it can handle a rich amount of biological detail at a low level of organizational complexity (e.g., behavioral and physiological ecology of individuals). Therefore, it does not require extensive a priori assumptions about which mechanisms are causally relevant. Rather, the IBM is used to generate long-term time series data via simulation "experiments" and that simulation output is used to identify which specific mechanisms drive system dynamics. Moreover, the theoretical foundation for translating simulation output into analytical theory is well developed (e.g., McCauley et al. 1993, Wilson et al. 1993, Durrett and Levin 1994, Bolker and Pacala 1997, Fahse et al. 1998, Grünbaum 1998, Wilson 1998). The factor most constraining the development of IBMs as mathematical tools for linking empirical research and analytical modeling is the dearth of detailed, empirical data to ground the structure of the IBM in biological reality (Grünbaum 1998). This paper illustrates the rich, new biological insight that can be gained when linking field ecology with an IBM.

I am primarily concerned here with the issue of scaling from behavioral-level interactions, which proceed very rapidly (on the order of minutes to hours), to population- and community-level interactions which proceed more slowly (seasons to years). Issues of scaling can involve one or more dimensions (space, time and organizational structure). I focus on time and organizational scale, although individual-level interactions do take on a local character owing to spatially explicit nature of the simulator. The structure of the IBM is inspired by insight gained from four years of field experimentation on old-field food webs (Schmitz 1994, 1997, 1998, Beckerman et al. 1997, Rothley et al. 1997, Schmitz et al. 1997, Schmitz and Suttle unpubl.). I show how empirical knowledge about short-term

plant resource choice and anti-predator behavior by herbivores can offer considerable insight into developing a working model of species interactions that emulates the outcome of short-term field experiments very closely. I then show how the IBM can be used to provide qualitative insight into the appropriate scale at which to begin developing analytical models that predict the long-term dynamics of the community.

Developing an IBM which offers key insights about natural systems requires a series of steps: 1) obtain empirical knowledge of the natural history and species interactions mechanisms from field research; 2) reproduce the natural history and mechanistic knowledge computationally; 3) calibrate the computational system to the field system; and 4) use the computational model to identify the dynamically relevant scale on which to base predictions of community dynamics. This paper is organized into sections that deal with each of the steps listed above.

## Empirical knowledge of the experimental system

### Natural history insights

My understanding of species interactions is based on research conducted in early-successional state old-fields at the Yale-Myers Research Forest in northeastern Connecticut, USA. The field supports 25 different grass and herb species. Average species richness per 0.25-m<sup>2</sup> sampling plot is 4.9. The dominant five plant species in rank order, where dominance is designated as any species whose biomass comprises greater than 1% of the total plant biomass, are the perennial grass *Phleum pratense*, and the perennial herbs *Solidago rugosa*, *Aster novaeangliae*, *Trifolium repens*, and *Daucus carota*. Together, these five species comprise 90.6% of the total vegetation biomass in 50 random 0.25-m<sup>2</sup> sampling plots. The numerically and biomass dominant leaf-chewing herbivore is the grasshopper *Melanoplus femurrubrum*. The major species of arthropod predators are the hunting spiders *Pisaurina mira*, *Hogna rabida*, and *Phidippus rimator*.

The dominant plant species are perennials which are present for about 190 d between early May and late October after which all above-ground biomass withers. *M. femurrubrum* grasshopper nymphs emerge in mid to late July (75–90 d into the season), become adults in mid to late August after passing through five instar stages and begin to die off in late September following breeding. *M. femurrubrum* overwinters in the egg stage.

We examined the consequences of manipulating spider density on interactions between *M. femurrubrum* and its plant resources. The spider predator exerted a strong indirect influence on plants via direct predator-prey interactions that reduced the density of the

grasshopper (density-mediated effects) and via changes in grasshopper foraging behavior in response to predation risk (trait-mediated effects) (Beckerman et al. 1997, Rothley et al. 1997, Schmitz et al. 1997). The details embodied in the spider-grasshopper-plant interaction inspired the rules used to develop an IBM of the experimental community. These details are described more fully in the next section.

## Mechanistic knowledge

### Behavioral-level detail

Field experiments demonstrated that grasshoppers select plant categories (grass and herb) as resources rather than individual plant species (Schmitz et al. 1997). Grasshoppers changed their per capita dietary proportion of grasses and herbs from an average of 70% grass when the predator was absent to 42% grass when the predator was present at average field densities (Rothley et al. 1997). The increased preference for herbs may be the result of grasshoppers seeking refuge from predation in structurally more complex herbs which tend to be spatially segregated from grasses in the field system (Beckerman et al. 1997). The shift in resource use by grasshoppers in response to the presence of predators is consistent with predictions from models of adaptive antipredator behavior of prey (Rothley et al. 1997, Abrams and Schmitz 1999).

### Population-level detail

To assay the relative importance of predation and predation risk on grasshopper populations, a series of experiments manipulated the modality of predator-prey interactions by rendering individual spiders incapable of subduing prey yet ensuring that they were still perceived by prey as a serious threat. The spiders' ability to capture and subdue prey was manipulated by gluing their chelicerae (feeding mouthparts) with non-toxic surgical cement. Such altered individuals were called Risk spiders. The impacts of Risk spiders on grasshopper population densities and trophic interactions were compared with the effects of natural spiders capable of capturing and subduing prey (termed Predation spiders).

Both Risk spider and Predation spider treatments indicate that spiders caused significant reductions in population densities of grasshoppers relative to the no predation control (Schmitz et al. 1997). This indicated that densities could be reduced by direct predation and indirectly perhaps via increased starvation due to reduced feeding time (McNamara and Houston 1987).

### Community-level detail

The ultimate goal of the field research was to understand the effect of antipredator behavior and predation on short-term interactions at the level of old-field inter-

action webs. The consequences of the antipredator behavior and predation on trophic interactions were examined by community-level experiments that altered the functional role of predators in community dynamics using Risk and Predation spiders in separate treatments.

Both Risk spider and Predation spider treatments had a significant positive indirect effect on grass biomass and a negative indirect effect on herb biomass (Fig. 1). The indirect effects of spiders on grass and herbs could be attributed largely to the shift in grass and herb resource selection in response to predation risk (Beckerman et al. 1997, Schmitz et al. 1997). Consequently, the indirect effects of spiders on plants, mediated by *M. femurrubrum* grasshoppers, arose largely from behavioral responses of grasshoppers to

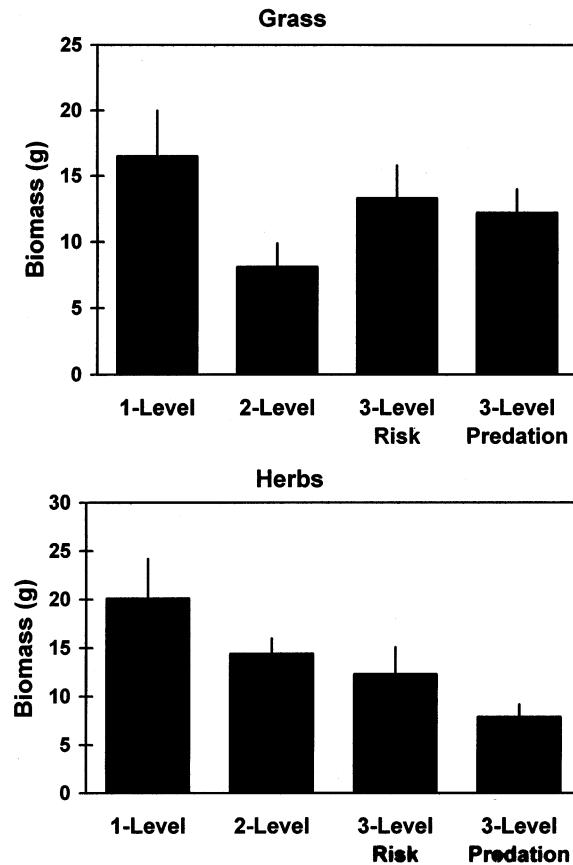


Fig. 1. Abundance of grasses and herbs in field experiments manipulating the number of trophic levels in a food web and the modality of spider predator effects (Risk vs Predation) on grasshopper herbivores. 1-Level represents 1-trophic level webs containing plants only, 2-Level represents 2-trophic level webs containing grasshoppers and plants, 3-Level represents 3-trophic level webs containing plants, grasshopper and spiders. Values are mean + 1 SE. The figure illustrates that spider predators have a positive indirect effect on grasses and a negative indirect effect on herbs largely mediated by grasshopper responses to predation risk (cf. 3-level Risk vs 3-Level Predation).

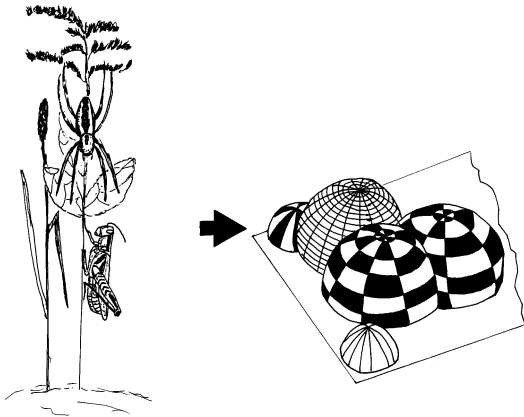


Fig. 2. Example of the landscape structure of Gecko. Gecko has a free-floating topology in which individual agents from different species (shown here as spheres with different color patterns) are denoted as spheres with their centers lying on the plane of the landscape. Agents are free to move in two-dimensional space and they have local interactions with other agents.

predation risk (a trait-mediated effect) rather than via reductions in grasshoppers density due to predation (a density-mediated effect).

The emerging insight is that information on grasshopper resource selection in the presence and absence of predators seems to be sufficient to explain the outcome of top predator manipulations on the experimental community, at least in the short term (within a season). Whether or not this translates into longer-term effects (over multiple years) is uncertain. This is exactly where the IBM can offer more insight. The next step, then, is to embed the natural history insight into a computational environment (Fig. 2) and use the mechanistic knowledge to define the rules driving the simulations. The IBM is validated before simulating the long-term dynamics of the food web by comparing the short-term outcome of simulation experiments with the outcome observed in field experiments that manipulated trophic structure of the food webs (Fig. 1).

## Reproducing natural history and mechanistic knowledge computationally

### The generic simulator

The computational platform used in this study is Gecko (Booth 1997, Schmitz and Booth 1997). Gecko is an individual-based, spatially explicit simulator that uses object-oriented rule sets to describe lower scale processes (e.g., behavioral and physiological ecology of individuals) and calculates the consequent higher scale (e.g., trophic) dynamics. Gecko represents a completely “bottom-up” modeling approach (sensu Langton 1988) because simulations are driven by assigning rule sets to individuals in the simulator at a very fundamental level

(physiology and behavior). These rules are fairly literal translations of the behavior of plants and herbivores under field conditions. Accordingly, the rules enable individuals to respond to stimuli in the computational environment in ways that emulate behavior observed under field conditions. The consequent population and community dynamics emerge as a consequence of individuals acting according to the rules.

The version of Gecko used for the current analysis is described in detail by Booth (1997). In Gecko, individuals undergo ungridded movement on a finite plane, i.e., a free-floating topology (Fig. 2). The landscape is defined by a rectangle within which a nutrient is supplied at a fixed rate (Fig. 2).

Individuals are denoted by spheres with their centers lying on the plane of the landscape and they are free to move in two dimensions (Fig. 2). Individuals have spherical volume that is specified by the radius  $r$ . The sphere has volume  $4/3\pi r^3$  and area  $\pi r^2$ . An individual's radius is proportional to biomass<sup>1/3</sup>. An individual's volume increases as resources are consumed, assimilated and stored. The rate at which an individual gathers resources is proportional to its area and, correspondingly, biomass<sup>2/3</sup>. To stay alive, individuals must gather sufficient resources to meet metabolic requirements. Metabolic rate is proportional to biomass<sup>3/4</sup>. Exponents used in scaling biomass to metabolic and resource consumption rates are based on standard allometric relationships (Peters 1983). Because metabolic cost increases faster with individual biomass than does resource intake rate, there are upper constraints on maximum volume that an individual can reach. Individuals can overlap in space, which denotes competition for local resources if the individuals belong to the same species or same trophic category, or consumer-resource interactions if individuals belong to different trophic categories. In the simulations described here, individual organisms belong to one of three trophic categories: plants, herbivores or carnivores.

Plants absorb nutrients directly from rectangles on the landscape. Plants undergo exploitative competition for nutrients. The magnitude of competition will depend on local plant density, local resource levels, and the size of individuals existing at a location. Local resource uptake is proportional to an individual's resource gathering capabilities, i.e., its area. Large individuals deplete the resource pool at a faster rate than do smaller individuals, so, larger individuals are at a competitive advantage when they overlap with smaller individuals. The proximate net effect of competition ranges from reductions in individual body size growth, to withering back in size and even death depending on an individual's physiological state (size of resource stores and metabolic costs) relative to local resource intake. The ultimate net effect of competition is a reduction in reproductive output or even an outright failure to reproduce owing to chronic shortages in resource intake.

Both herbivores and carnivores have perception and intent that stimulate movement on the landscape. Movement is governed by different rules for herbivores and carnivore, but it is effectively a biased random walk with reflecting boundary conditions (Grünbaum 1998, Turchin 1998).

When herbivores move, they actively search for resources (plants) within a designated search path width that scales to their body size radius. Herbivores move a distance equal to their body size radius each time step. Directional movement is steered by a “veer” function, i.e., they move forward in the general cardinal direction they face plus or minus a maximum of  $\frac{1}{2}$  veer. For example, if veer is preset to  $\pi$ , herbivores randomly veer no more than  $\pi/2$  radians ( $90^\circ$ ) left or right of their current heading. In each time step, herbivores select the individual plant within that search path that yields the highest rate of resource intake to maximize the chance of meeting demands for maintenance, growth, and reproduction, i.e., maximize individual fitness. Hence, the biased random walk is driven by adaptive resource selection behavior of the herbivore. The herbivore takes a discrete “bite” out of the plant. The size of the bite taken is proportional to the herbivore’s radius. Herbivores add consumed resources to their own body stores (thus increasing their own volume). Plants lose that amount of resource causing their volume to shrink; hence plants are never completely consumed or directly killed by herbivores. Herbivores also have a predator detection radius that is a multiple of their body size radius. The detection radius allows them to sense an oncoming predator and attempt to evade it by moving in a safe direction (see below) away from the oncoming predator.

Carnivores have an attack radius, which is a multiple of their body size radius. They also have a much larger smell radius, also a multiple of body size, which allows them to detect and then actively hunt prey. Predators search randomly until a prey item is detected within the smell radius. The predator then moves directly toward that prey item. Prey are captured if their volume falls within the predator’s attack radius. Here the biased random walk is driven simply by prey detection and opportunity for capture.

In many IBMs, the focus of time is on reproduction, hence a time step is equivalent to a generation. In Gecko, the focus of time is on feeding, so a time step is best envisioned as a portion of a day equivalent to a foraging bout (e.g., one to several hours). In the simulations used here, a day is comprised of 10 feeding periods. The landscape produces resources incrementally each time step. Within each time step, resources are consumed in discrete units by plants and animals.

Each individual requires several units of prey resources to convert into a unit of their own body tissue. This conversion efficiency, which varies with trophic category of the organism, generates classical pyramids

of numbers and biomass in the food web (Schmitz and Booth 1997). I assumed that 10% of abiotic resources taken up by plants are converted into plant tissue, 33% of plant tissue is converted into herbivore biomass, and 85% of herbivore biomass is converted into predator biomass. The conversion efficiencies are based on average estimates reported for these terrestrial trophic groups (Hairston and Hairston 1993) but they can be varied for simulation purposes. Individuals reproduce once they have garnered sufficient resources to pay metabolic and growth costs, which may require several feeding time steps. Hence, movement, foraging and reproduction are not synchronous in each time step. Indeed, individuals may require up to 100–200 d (1000–2000 time steps) to gain sufficient resources for reproduction. Thus, generation time is on the order of a natural season in the simulations. Moreover, some individuals may fail to gain sufficient resources for reproduction by the end of a simulated season and so do not reproduce.

Organisms undergo asexual reproduction when their size exceeds a minimum breeding volume. Offspring are endowed with a supply of resources that determines their body size radius. The size of the endowment depends on the extent to which a parent’s resource pool exceeds the parent’s breeding radius. Offspring are placed at a random distance outside their parent’s radius according to the function: distance = (parent radius + offspring radius)<sup>random[0...1]</sup>. This function guarantees that parent and offspring never overlap in space immediately after reproduction. Offspring are also placed in a random cardinal direction from their parent.

Organisms die when they cannot pay metabolic costs. Dead organisms are recycled back into the nutrient pool of the landscape. Hence, this is not a completely open system.

Stochasticity enters the simulations in several ways. First, it arises from the initial random seeding of organisms onto the landscape. This causes the initial time series to undergo transient dynamics that are artifacts of the initial conditions. However, extensive simulation (i.e., 100 runs of the simulator) in which initial starting densities of all species are varied systematically by up to 50% indicates that the initial transients die out after 50 to 60 d of the first season (i.e., 500–600 time steps). To remove artifacts of transients, I did not include data for the first simulated season in all time series analyses. Second, although movement of organisms in space is qualitatively directional, there is a random component due to the veer function. The degree of stochasticity varies positively with the veer angle. Third, the strengths of local species interactions are emergent properties of the number of individuals that occur locally in space and the size of the resource pool at a given location. The exact local interactions are not reproducible among runs of the simulator. Finally,

reproduction is stochastic because it depends entirely on local resource uptake over consecutive time periods. Also, offspring are placed away from their parents according to an exponential probability function.

### **Simulation rules based on natural history and field experiments**

Understanding the causal relationships that may determine the long-term structure and dynamics of species in the field requires building a model food web that emulates environmental conditions of the real-world food web. Accordingly, the rules used to drive the simulations must reflect many of the important attributes of the field system as revealed by the short-term experiments. For the old-field system, these attributes are seasonality, three functionally distinct trophic levels, and predator effects on the plant community mediated by herbivore density and behavior.

Temperate old-fields have a strong seasonal component that effectively can be divided into two main periods, a growing/reproducing period and a dormant period. During the growing period, plants and animals complete their life-cycles and then either wither, die or remain dormant until the following growing period. The exact way that plants and animals pass through the dormant period depends on the species. All of the plant species are perennials in which case above-ground biomass withers in autumn and it is recycled via the detrital chain leaving a dormant root stock below ground. The plants also produce seeds that lie dormant in the soil until the next growing period. The grasshoppers develop from nymphs to adults, reproduce and lay eggs in the soil at the end of the growing period. All adults die but the eggs lie dormant and hatch during the following growing period. The spiders tend to overwinter in the litter layer as juveniles and emerge, ready to prey on insects, in the following growing period.

I incorporated seasonality into the computational model by dividing a season into a growing period of 1900 time steps (i.e., 10 “hours” per day  $\times$  190 d) and a dormant period of 1 time step. In the simulations, all plants initiate growth at the beginning of each growing season. At the end of the growing season, surplus resources are allocated to seed production and living plants then wither back to the center point of their location. Any seeds that were produced during the 190-d growing season germinate and grow; seeds produced at the end of the season remain dormant until the next growing period. Because of physiological constraints, however, plants tend to grow vegetatively (increase volume) throughout the growing season and produce the majority of their offspring (metaphorical seeds) at the end of the season, provided there are sufficient resources for offspring production. All plants initiate growth from their center point on the landscape in the following growing period.

Herbivores are introduced into the environment after 80 d (800 time steps) of each season to emulate the emergence times in the study field. Emergence times in nature vary because abiotic conditions can accelerate or retard egg development. This stochastic element was not included in the simulations here. The field research indicated that statistically similar outcomes of trophic interactions occurred among years despite variations in hatching times of the herbivores (Beckerman et al. 1997, Schmitz et al. 1997). Thus, for a starting approximation, I assumed that this stochastic element could be safely abstracted as a constant. In the simulations, herbivores pass through three stages: early juvenile, late juvenile and adult. In reality, there are five stages but they can be collapsed to three stages because grasshopper instars effectively can be grouped according to size and resource demands (e.g., early juvenile = instar I-III, late juvenile = instar IV-V [Schmitz et al. 1997]). The herbivores must accrue enough resources to pass through each life-cycle stage; and they can only reproduce as adults. Reproduction depends upon the size of resource stores accrued by adults which in turn depends upon resource intake. As a consequence of local variation in resource availability coupled with the restricted season length, some adults are able to produce multiple clutches in a growing season whereas others may not reproduce at all. Initially, herbivores are seeded randomly onto the landscape. Emergence and population growth in subsequent seasons depends on the spatial location in which eggs were laid in the previous growing season.

For the purposes here, predators that emulate spiders do not undergo population dynamics. Rather, they are treated as a component of the environment of the plant-herbivore interaction by simply having a constant density of predators in each season.

The computational community contains two species of plants, a herbivore that selects between the two plant groups and a carnivore that preys on the herbivore.

The plant species are defined from the herbivore’s perspective. Recall that under natural conditions, grasses are the most nutritious plants and they are preferred by grasshoppers. However, grasshoppers avoid these plants when faced with predation risk and seek out less nutritious herbs to avoid predation. In the simulations, the first species, termed “preferred” plant, is highly nutritious and it is intended to emulate grass. The second is less nutritious but it represents a refuge from predation and is thus termed “safe” plant. The safe plant emulates herbs. The two plants create a trade-off situation similar to the one observed in the field. The preferred plant is highly nutritious but there is a risk of predation associated with feeding on that species. The safe plant is less nutritious but it has no predation risk.

I initially explored dynamics using two classes of herbivores: nonadaptive and adaptive. Nonadaptive herbivores do not recognize that predators pose a threat and therefore they take no action to avoid predators. This type of herbivore eats only the most nutritious plant resource. However, while calibrating the simulator I discovered that nonadaptive herbivore populations never persisted beyond half of the first season because of predation and this outcome was invariant to changes in predator densities. Consequently, I excluded nonadaptive herbivores from all further simulation experiments.

Adaptive herbivores, on the other hand, were designed to respond to the presence of predators. Adaptive herbivores attempt to seek out and utilize the preferred plants whenever possible to maximize their reproductive output. They should only retreat to safe plants when confronted by predation threat. Predation threat is signaled when the predator enters the herbivore's detection radius. In this scenario, smaller (younger) herbivores will have smaller detection radii and therefore they have less time to evade predators (greater risk) than do larger herbivores. Herbivores on safe plants will continue to eat safe plant biomass until the predator moves beyond their detection radius. At this point, the herbivores deem it safe to leave the safe plant and resume feeding on the preferred plant.

There are two classes of predators used in the simulation experiments. These predators differ in their modality of effect. The first, predation predators, are capable of capturing and subduing the herbivore prey much like spiders under natural conditions. The second class, risk predator, can only scare prey, much like the spiders with glued mouthparts in the field experiments. This distinction in predator modality allowed the separation of effects due to predation and predation risk on the short- and long-term dynamics of the computational ecosystem.

During the course of calibrating the simulator I discovered that adaptive herbivores went extinct by the middle of the second season in food webs containing predators, adaptive herbivores, and preferred plants only. This occurred because adaptive herbivores did not have a refuge from predation. The likelihood of extinction by the end of the second season did not vary with predator density. Also, herbivore populations in three-level food webs containing only safe plants did not persist beyond three seasons. In this case, the herbivores were not eaten by the predators but the comparatively poor nutritional quality of the safe plant resulted in such a low reproductive output that the herbivore population could not persist. As a consequence, all simulation experiments involving two- and three-trophic level food webs contained both preferred and safe plants.

## Anatomy of the time series and data sampling

In *Gecko*, each realization of a simulation can generate a time series of species density or biomass within and among seasons (e.g., Fig. 3). Plants reached a steady state set either by resource supply rate (e.g., safe plant, Fig. 3) or by limitation due to herbivory once herbivores entered the system (e.g., preferred plant, Fig. 3). Simulation experiments indicated that the rate of plant population growth to the steady state is density dependent. The population growth to a steady state emerged as a consequence of individuals acting according to simulation rules, not because there is a numerical maximum level of plants being set in the IBM (Schmitz and Booth 1997). Herbivores emerged as early instars at high densities and declined in abundance as they developed through their various instar stages (Fig. 3). This pattern again emerged from the simulations because individual herbivores had increasingly higher demands for resources as they grew through various instar stages while at the same time their resource base declined in abundance (Fig. 3). A series of simulation experiments indicated that the rate of herbivore population decline to the steady state was density dependent. This within-season pattern of emergence and population decline in each realization of the simulator matched the pattern routinely found for grasshopper populations under natural field conditions (Ritchie and Tilman 1992, Belovsky and Slade 1993, 1995, Schmitz 1993, 1997).

In the old-field study system, the experiments were terminated at the end of each growing season, after the herbivores and plants reached a steady state abundance and before the onset of an insect-killing frost. Plant and herbivore species abundances were sampled at this time to evaluate the direct and indirect effects of spider predators on the abundance of plants in the experimental old-field community. A steady state similar to that found in the field emerges in the realizations of the IBM (Fig. 3). In order to compare the IBM output with the results of the field experiments, I emulated the field protocol by sampling the simulated time series when herbivore and plant densities simultaneously were in a steady state (i.e., at the end of the season, Fig. 3).

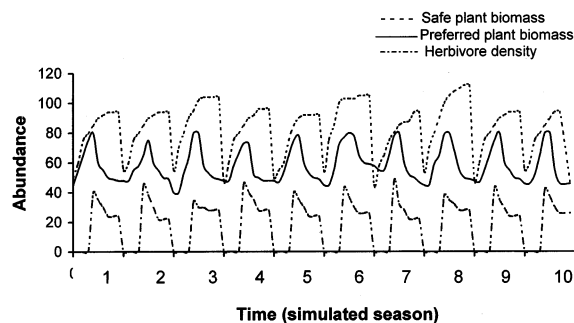


Fig. 3. Example time series for preferred plant, safe plant and herbivore abundance (virtual biomass) over 10 consecutive 190-d growing seasons in a single realization of *Gecko*.

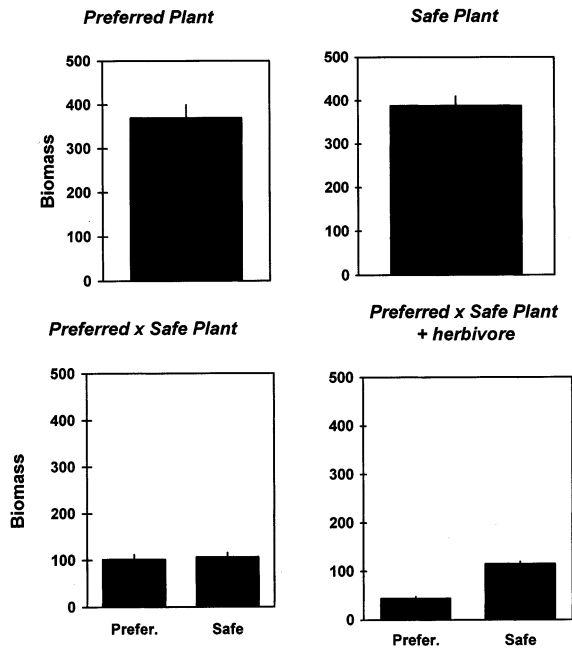


Fig. 4. Short-term (single season) steady-state densities in systems with either the preferred or safe plant alone, both plants together or both plants with the herbivore. The simulations indicate that the two plants compete for resources and that herbivores mediate the competitive outcome through foraging.

### Short-term simulation experiments

I systematically increased trophic complexity of the IBM to understand its effect on species interactions in the computational system. I conducted a series of short-term (1-season) simulation experiments with the following treatments: 1) preferred plant alone; 2) safe plant alone; 3) preferred + safe plant; 4) preferred and safe plants + herbivores; 5) preferred and safe plants + risk predators; and 6) preferred and safe plants + predation predators. Because Gecko is a stochastic simulator, I obtained 10 realizations (the first season transients were removed from each realization) for each treatment and calculated the mean and standard error for the simulation outcome. Ten realizations were chosen for two reasons. First, in designing the simulation experiments I ran 50 realizations of the simulator but found that the sampling variance in species steady state density among realizations stabilized after eight to ten realizations. Second, the aim of this exercise is to emulate field experiments using simulation experiments and the maximum level of replication in the field experiments in any one season was ten (Beckerman et al. 1997, Schmitz et al. 1997).

In realizations with each plant species alone (allopatric), both preferred and safe plants reached the same mean steady state abundance (Fig. 4). In simulations with both plant species coexisting, (sympatric), their

densities were much lower than allopatric densities (Fig. 4), as a consequence of competition for a limiting nutrient supply. This arose because of the spatially explicit nature of the simulated landscape. Under allopatric conditions, each species became a vast monoculture distributed evenly across the landscape. In sympatry, local between-species interactions created patches largely containing one plant species or another.

Herbivores affected the steady state densities of the coexisting plants (Fig. 4). Preferred plants had a 60% decrease in abundance due to herbivory. Safe plant densities were unaffected because, in the absence of predators, herbivores did not feed on these plants. Moreover, there was no increase in safe plant abundance due to competitive release because of the spatially explicit structure of the plant species distributions. Safe plants could not rapidly compensate by expanding their distribution on the landscape within the span of a short growing season. Note, however, that this is a consequence of examining dynamics in a single season. Simulations over multiple seasons (discussed below) illustrate that safe plants do respond to decreased competitive pressure from preferred plants over the longer term.

The addition of predators to the computational systems resulted in an increase in abundance of preferred plants relative to the system with herbivores and plants only (Fig. 5). In the short term, the indirect effects of predation predators on each plant species matched those of risk predators even though each type of predator had a different direct effect on herbivore density (Table 1). This illustrates that mediation of predator effects on plants via behavioral shifts of herbivores (trait-mediated effects), rather than reductions in herbivore density (density-mediated effects), can explain the top-down effects of predators on plants. This result is consistent with observations from field experiments (cf. Figs 1 and 5).

The congruence between the simulations and field experiments indicated that the simulator could reliably reproduce the outcome of short-term species interactions under field conditions. This increased the confidence that the simulator might offer reliable insight into long-term dynamics of the natural field system. The next section details simulation experiments that were conducted to identify how seasonality and processes operating at the individual behavioral level and at the population level contribute to the long-term dynamics of the computational food web.

### Identifying the dynamically relevant scale for predicting long-term dynamics

I examined whether or not top predators could have a bearing on the long-term dynamics of the computational system by conducting a series of perturbation



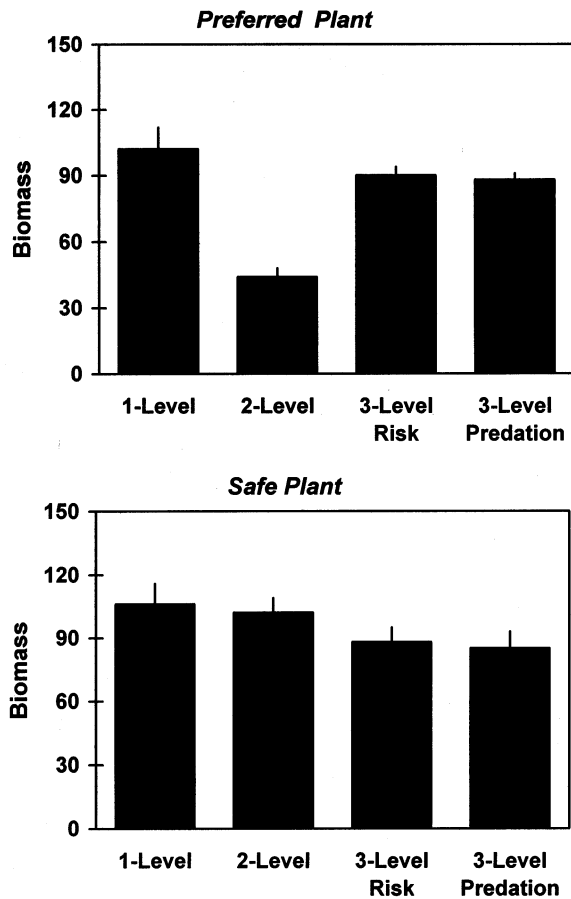


Fig. 5. Outcome of short-term simulations which manipulated trophic structure and modality of predator effects. 1-Level represents 1-trophic level webs containing plants only, 2-Level represents 2-trophic level webs containing grasshoppers and plants, 3-Level represents 3-trophic level webs containing plants, grasshopper and spiders. Values are mean + 1 SE. Predators appear to have a positive indirect effect on preferred plants and a weak negative indirect effect on safe plants. The predator effects appear to be mediated by herbivore responses to predation risk (behavior-level response) rather than reductions in herbivore density due to predation (population-level response). The simulation outcome matches that observed under field conditions (see Fig. 1).

experiments that manipulated the abundance of top predators. The long-term window for each realization of an experimental treatment was 10 seasons, the equivalent of 19000 time steps (days). A period of ten seasons was a compromise. I ran 10 replicates of each

Table 1. Steady-state herbivore densities under different treatments in simulations of short-term (single season) trophic interactions in the Gecko simulator. Values are mean  $\pm$  1 SE.

| Treatment           | Density         |
|---------------------|-----------------|
| Control             | 40.2 $\pm$ 1.1  |
| Risk predators      | 24.6 $\pm$ 0.79 |
| Predation predators | 20.8 $\pm$ 1.1  |

realization producing 190000 data points for each of three species in each simulation experiment. Collection of data beyond ten time periods resulted in disk storage problems, given the magnitude of information generated by the IBM over several realizations. Ten consecutive periods has been considered the minimum time scale needed to understand the long-term dynamical behavior of a natural system (Turchin 1990). I calculated a mean and standard error for the ten realizations in each simulation experiment.

I conducted two simulation experiments. The first experiment compared food web dynamics containing 1) both plant species and the herbivore (Control) with dynamics of food webs containing 2) both plants, the herbivore and the risk predator and 3) both plants, the herbivore and the predation predator. This experiment examined the long-term indirect effects of predators on community structure and dynamics resulting from direct effects of predators on herbivore behavior and on herbivore density. The second experiment began with both plant species and the herbivore. I then introduced either the risk predator or the predation predator at the beginning of the second season. The dynamics in this system were compared with the dynamics in the first experiment to assay how quickly the transient dynamics resulting from the mid-course predator introduction died out.

In the first experiment, both plant and herbivore population densities settled into a particular state within the first three seasons and remained in this state for the remaining seven seasons (Fig. 6) (there were slight interannual fluctuations in steady-state density but usually within 15% of the mean). Herbivore density in each season matched the outcome for the short-term experiments, i.e., densities were on average 1.7 times greater in the absence of predators than in their presence and grasshopper densities in the presence of risk predators were on average 1.2 times higher than grasshopper densities in the presence of predation predators (Table 1). In food webs with plants and herbivores only, the herbivores devastated the density of preferred plants. This released the safe plant from interspecific competition allowing its population to increase in size over the long term (Fig. 6). In food webs with plants, herbivores and predators, the predators had a positive indirect effect on preferred plants. This caused the abundances of preferred and safe plants to equalize and remain so over the long term (Fig. 6). Moreover, the abundances of the two plant species were similar under risk and predation predator treatments even though the predator types had differential effects on grasshopper population density (Table 1).

In the simulations, predation predators did not just prey on herbivores; they also stimulated antipredator behavior. In order to quantify the contribution of these two components on community dynamics I partitioned the effects due to predation from effects due to behav-

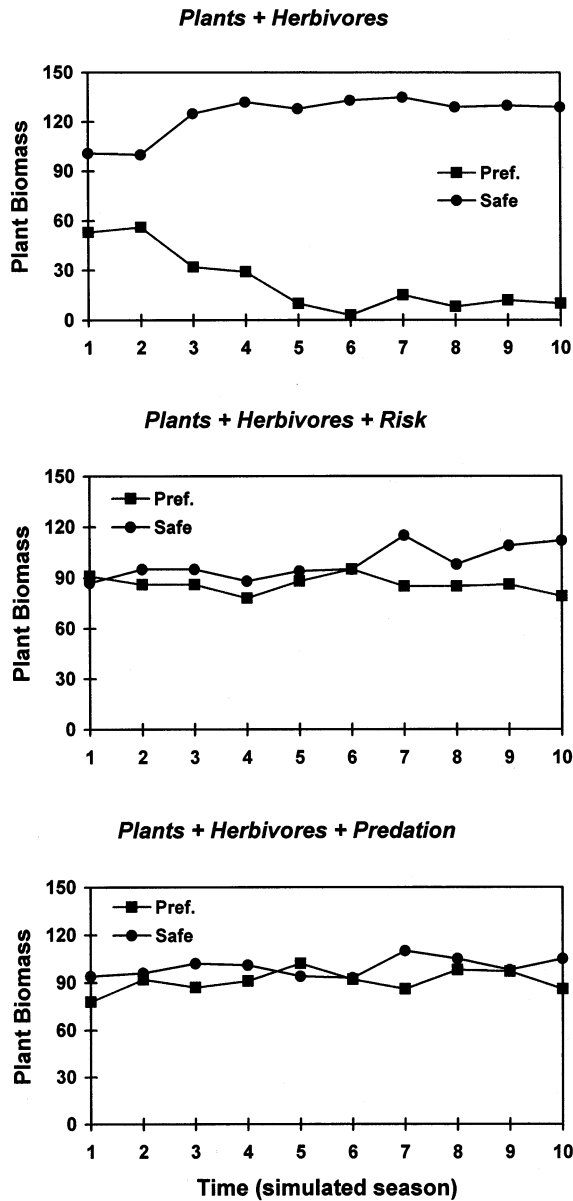


Fig. 6. Example of a long-term time series of steady state biomass of preferred and safe plants in response to simulated trophic manipulations. The simulations involved baseline runs for 2-level webs containing herbivores and plants and manipulations of the baseline with the addition of Risk predators or Predation predators.

ioral responses of herbivores using the risk predator treatment as a basis for comparison. For each of the ten seasons in each of the ten realizations, I estimated the percentage loss or gain in herbivore and plant abundance due to antipredator behavior of herbivores using the formula  $A_C - A_{RP} / (A_C - A_{PP})$  where  $A_C$ ,  $A_{RP}$ , and  $A_{PP}$  are, respectively, herbivore or plant abundances in the control, in the risk predator, or the predation predator treatments. Predation risk alone

accounted for a substantial amount of variation in herbivore abundance and the majority of variation in plant abundance (Table 2). The asymmetry in effect between preferred and safe plants was due to differences in the herbivore behavior on those plants. Herbivores fed continuously on preferred plants when it was safe to do so. Herbivores only retreated to safe plants when there was an immediate threat of predation. While on a safe plant, herbivores remained vigilant for one feeding bout to determine if it was safe to return to a preferred plant. Herbivores only began feeding on safe plants if the predation threat in the vicinity of that safe plant persisted. Consequently, herbivores did not inflict the same level of damage on the safe plants as on the preferred plants.

The effects of predation and predation risk can carry over from one season to the next because of density changes and life-history shifts in populations that manifest themselves over time. To understand how this carry-over effect might be manifest, I examined the autocorrelation structure of the time series generated by each realization of the simulator. In the majority of cases, the abundances of herbivores (Fig. 7) and plants (Fig. 8) were weakly correlated among seasons if correlated at all. The exception was a one season lag in effect of herbivores on preferred plants in the community containing only plants and herbivores (Fig. 8).

In the second experiment, the transient effects of introducing predators in the second season died out by the end of the third season (Fig. 9). Also, densities of plants and herbivores in the three-trophic level systems in this experiment rapidly converged on the densities observed in the corresponding three-trophic level systems in the first experiment (cf. Fig. 6). Again, this rapid outcome could largely be attributed to the behavioral shifts of the herbivores in response to the introduction of the predators.

### Summary of simulation results

The autocorrelation structure in the time series indicated that there was very little, if any, serial dependence in herbivore or plant abundance among seasons. This can be attributed to seasonality which caused an abrupt halt to the herbivore and plant population trajectories and "reset" the system at the beginning of each new

Table 2. Variation in within-season herbivore and plant abundance attributable to herbivore responses to predation risk in realizations of the Gecko simulator. Values are mean  $\pm$  1 SE.

| Response variable       | Variation explained (%) |
|-------------------------|-------------------------|
| Herbivore density       | 42 $\pm$ 7.3            |
| Preferred plant biomass | 94 $\pm$ 3.2            |
| Safe plant biomass      | 70 $\pm$ 9.8            |

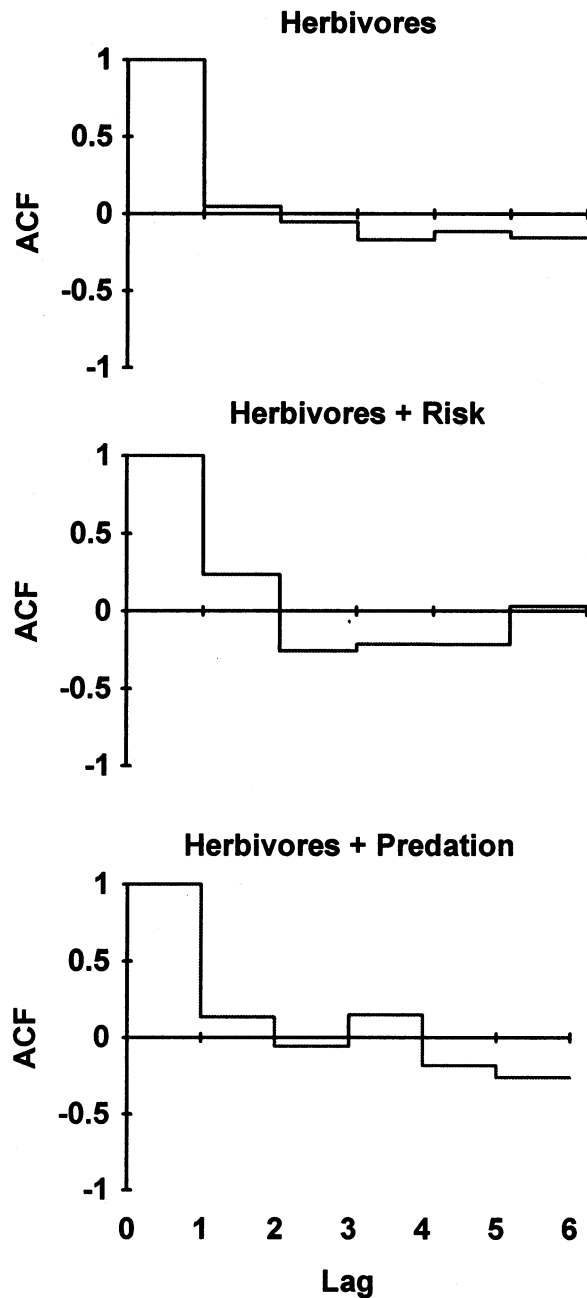


Fig. 7. Autocorrelation structure in time series of herbivore density in relation to different simulated trophic manipulations. ACF represents the autocorrelation value for time series comparisons with time lags (Lag) of zero to 6 yr.

season (Fig. 3). As a consequence of seasonality, within-season (short-term) species interactions had an overpowering influence on community structure. Moreover, it was the risk avoidance behavior of herbivores, and its attendant impacts on each plant species, that accounted for the majority of variation in community structure within each season. Thus, community struc-

ture was a highly predictable consequence of simply knowing the short-term resource selection behavior of the herbivores in the absence and presence of predators. The long-term dynamics of the community emulated here can then be interpreted as being a concatenated string of short-term, highly predictable, events that converged on similar steady states over consecutive seasons (Fig. 3).

## Discussion

This study illustrates how field data linked with an IBM can lead to new insights about the role of individual behavior in dynamics of a food web. In this context, the IBM serves as an intermediate step in theory development. This modeling philosophy differs from the alternative approach in ecology, which is to skip the simulation step and embed behavior directly into analytical models (e.g., Abrams 1992, 1995). However, when beginning with an analytical construct, it must be assumed that there is a very clear understanding of the underlying causal relationships between short-term behavior and long-term community dynamics. If this understanding is absent, which it usually is, the analytical model cannot clarify whether or not behavior should be included in an analytical construct. Rather the model merely reveals how behavior affects dynamics relative to analytical models that do not include behavior. The advantage of an IBM is that, once it is calibrated to a field system, it can help resolve how short-term behavioral effects might be transmitted across organizational and temporal scales. If behavior has an important bearing on long-term dynamics, then the IBM can help reveal the underlying causal relationships that produce this outcome. Such information will then inspire the correct mathematical formalism for an analytical model. If behavior does not have visible consequences at population and community scales, then the IBM can help to identify the processes by which behavioral effects are attenuated.

The simulation results presented here illustrate that community dynamics became highly predictable despite the trophic complexity of the system. The predictability was a result of seasonality acting as a strong forcing variable on the system. Seasonality removed the serial dependence in population abundance over time, such that long-term dynamics effectively became a chronological sequence of independent, short-term events. As a consequence, processes operating over the short term (behavioral responses of individuals) played a much stronger role in shaping long-term community structure than longer-term processes (density responses).

The regularity in a time series generated by seasonal effects is known to enhance the ability to forecast (Box and Jenkins 1976). However, accurate predictions re-

quire time series data to be collected at intervals that reflect the time scale of species interactions. In the simulated food web, the high predictability arises because data were collected *within* each season, not just among seasons. The importance of choosing the dynamically relevant sampling period is often overlooked: most ecological time series derive from annual (between-season) sampling because it is automatically assumed that the dynamically relevant events occur among seasons or because repeated sampling within seasons is too prohibitive. However, ignoring the information value of within-season interactions may lead to the wrong interpretation about community dynamics and thus decrease our ability to elucidate causality. For example, the absence of history in the annual time series (Figs 7, 8) would suggest that there is little or no density dependence in the population dynamics of plants and herbivores over the course of ten seasons. This perceived lack of density dependence often leads to the conclusion that the community cannot possibly

reach a long-term steady state or equilibrium, which argues for a nonequilibrium view of community dynamics. Examining dynamics within a season, however, reveals that failing to identify density dependence in interannual time series does not preclude the possibility that density dependence has a strong hand in shaping community structure. Within a season, there is strong spatial and temporal density dependence operating in the plant and herbivore populations because the rule structure of the simulator predisposes this outcome. For example, herbivore populations declined because of stage-structured resource demands for increasingly limited resources (Fig. 3). Also, spatial density dependence led to intra- and interspecific plant competition (Fig. 4). Moreover, a particular community reaches a steady-state in each season and the steady-state values are very similar among seasons (Fig. 3).

The implication of this is that deeper insight into community dynamics may require looking deeper into the organizational structure of communities in order to

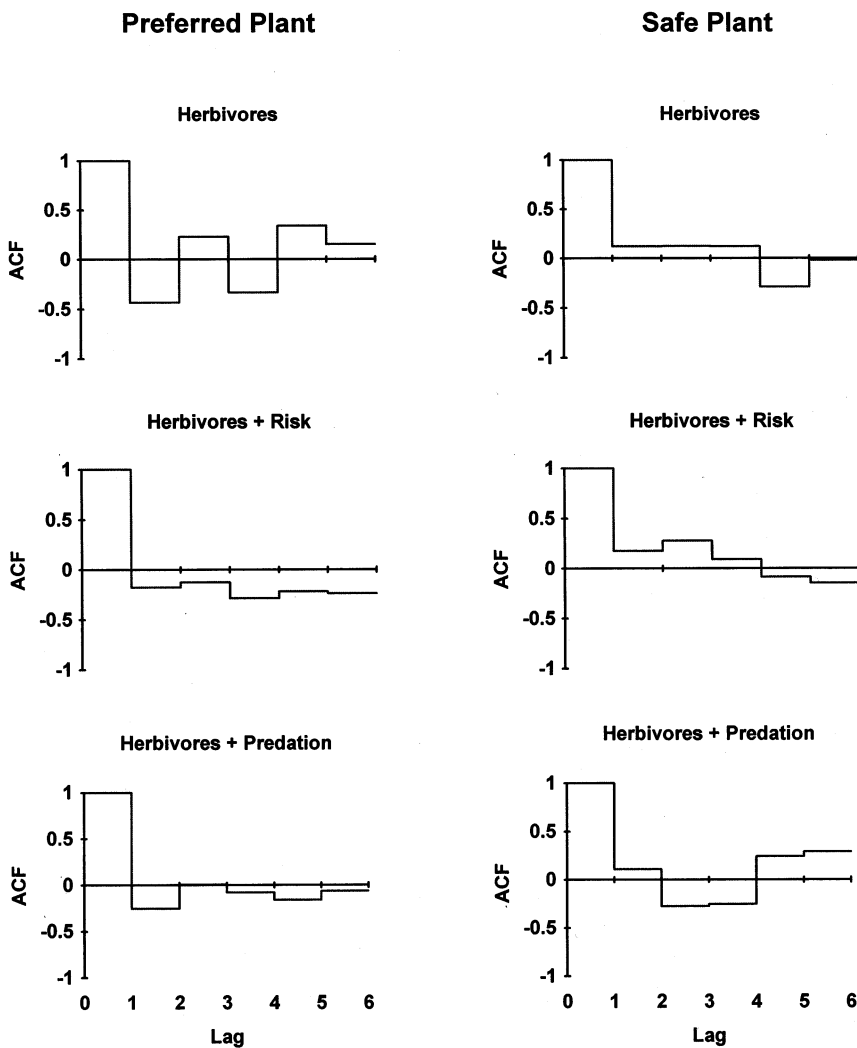


Fig. 8. Autocorrelation structure in time series of preferred and safe plant abundance in relation to different simulated trophic manipulations. ACF represents the autocorrelation value for time series comparisons with time lags (Lag) of zero to 6 yr.

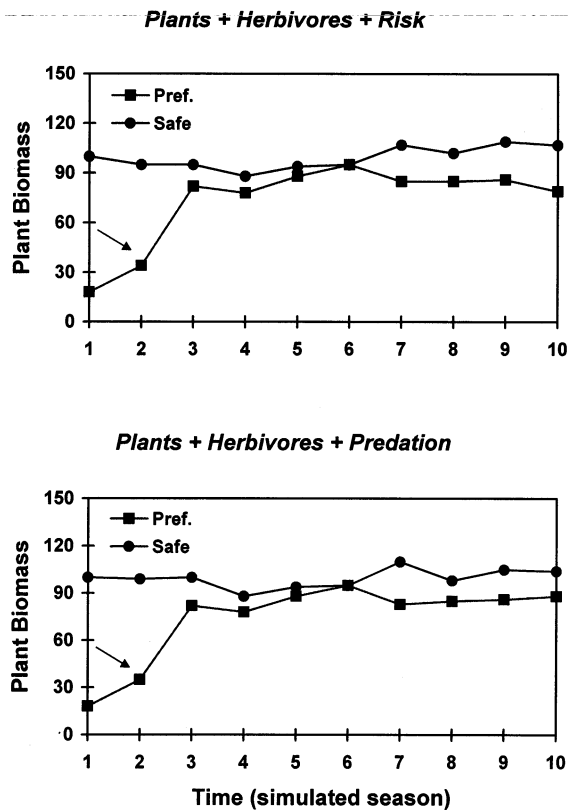


Fig. 9. Effects of adding Risk predators or Predation predators in season 2 on the long-term dynamics of preferred and safe plants in the simulated community. The figure illustrates that the plant biomass converges rapidly (within 2 seasons) on a new steady state.

derive the appropriate mechanistic insight into species interactions. This does not imply that yet another layer of reductionism must be added to understand higher-scale community dynamics (see Łomnicki 1992). Rather, the individual level is the dynamically relevant organizational scale in the study system. And so, it would not be universally appropriate to abstract faster scale mechanisms into analytical models describing slower scale population dynamics by assuming behavior has reached a stationary state (cf. Fahse et al. 1998).

At the same time, the simulation results of this particular study cannot be used to make the general statement that behavior matters in all systems. This is a drawback of all simulation approaches. One can only begin to generalize after the simulation output is translated into analytical theory and only then when it can be shown that IBM models emulating different kinds of systems can be described by the same class of analytical model. However, the insights generated from the IBM process used to understand long-term dynamics have some general implications. First, a rule-based IBM approach can lead to critical insights about community dynamics. Second, whenever individual behavior plays

an important role in community dynamics, and it is increasingly becoming apparent that it does (e.g., Turner and Mittelbach 1990, Huang and Sih 1991, Rosenzweig 1991, Werner 1992, McIntosh and Townsend 1996, Werner and Anholt 1996, Beckerman et al. 1997, Peacor and Werner 1997, Peckarsky and McIntosh 1998, Schmitz 1998), understanding the particular behavioral details of the species interactions can increase the ability to predict community-level dynamics. Third, whenever individual behavior has an overriding effect on community dynamics, it may not be sufficient to account for behavior by abstracting it as a function in models describing population-level interactions. Rather, it becomes imperative to incorporate behavior by treating it as a state variable at the individual level (e.g., Rosenzweig 1991, Abrams 1995, Peckarsky et al. 1997).

Ecologist are continually challenged to characterize the dynamics of natural systems using mathematical models. Deriving an appropriate model of system dynamics can be a long and iterative process whose outcome depends critically on the quality of empirical data describing the long-term behavior of a natural system. Most ecological time series are insufficient to offer insight into the way species interactions at different organizational scales contribute to the long-term dynamics of natural communities. An IBM approach is a powerful way to help resolve this difficulty. It provides an intermediate step in theory development by linking information on mechanisms of species interactions directly from experimental field ecology to the theory development process. Once calibrated to the real-world field system it can provide the quality of time series data needed to identify which organizational and temporal scales may be relevant to describe the dynamics of a particular community.

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