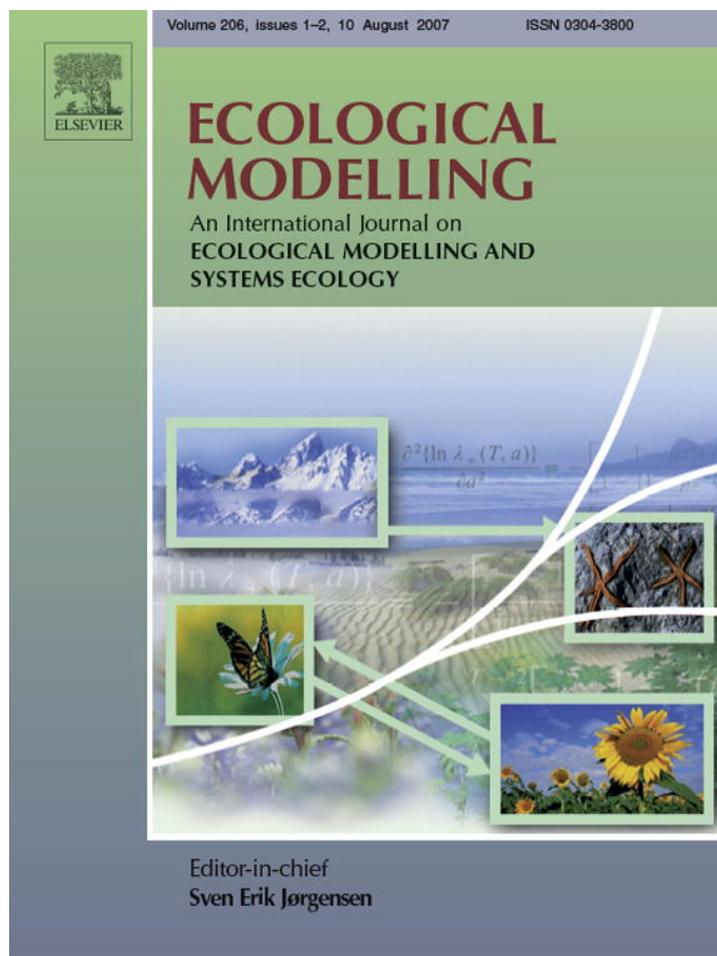


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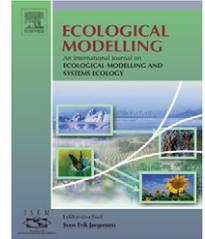
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# Consequences of body size variation among herbivores on the strength of plant–herbivore interactions in a seasonal environment

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## ABSTRACT

Classical theory in community ecology assumes that smaller-scale details such as individual traits can be abstracted safely and that community dynamics can be simply characterized in terms of net changes in population densities. Here we use a mechanistic simulation model of a three-level food web to explore the effect of initial body size variation among herbivores on final plant abundance resulting from a non-linear relationship between population demography and body size. We show that initial herbivore body size variation has a negative effect on their survival and consequently a positive effect on the final plant biomass. We then use trait distribution, in combination with body size-survival and body size-fitness curves estimated through simulations, to generate predictions for comparison with observed food web effects. We show that, owing to frequency-dependence, our ability to predict herbivore population dynamics is limited. However, at the community-level, this frequency-dependence, as well as changes in herbivore population size, can be abstracted safely and the strength of plant–herbivore interactions can be simply predicted from initial body size distribution in combination with the survival curve. Our findings suggest a need to revisit classical theory in community ecology. Doing so will require the mechanistic study of population demography and experimental testing of the effect of trait variation on community dynamics.

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## 1. Introduction

The way in which different organizational levels (e.g., individual, population, community) combine to influence population and community dynamics remains a fundamental research question in ecology (Lomnicki, 1988; Rosenzweig, 1991; Abrams, 1995; Werner and Anholt, 1996; Levin et al., 1997; Peckarsky et al., 1997; Schmitz, 2001; Pfister and Stevens, 2002, 2003). This question is motivated by the need to

understand to what extent mechanistic complexity of biological systems must be included in theory, and how much can be abstracted safely while still achieving biologically faithful and quantitatively accurate generalizations of community dynamics. Classical theory in community ecology has resolved this question by assuming that it is sufficient to abstract individual-scale detail and characterize dynamics simply at the population level in terms of net changes in densities.

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In making such an assumption, however, one must recognize that fundamentally a population is a conceptual abstraction of an ensemble of individuals. In other words, individuals have traits such as age, size, physiological condition, or energetic state that influence their behavioral responses. Moreover, they show a life history performance in different ecological milieus that arises from variation in the abundance of competitors, predators and required resources (McCauley et al., 1993; McPeck and Peckarsky, 1998; Ovadia and Schmitz, 2002; Pfister and Peacor, 2003). Changes in life history, in turn, affect population demography, which could have a profound effect on the dynamic character of a system. Thus, a critical starting point in theory development is deciding how best to represent individuals in a theoretical construct. Describing dynamics at the population-level means that we ignore the higher moments of trait distribution and consider only the mean trait value. A key question is whether and when it is necessary to consider higher moments of trait distribution such as variation.

There is a growing sense among ecologists that higher moments of trait distribution cannot be neglected when the trait translates non-linearly into per capita population growth rate (e.g., non-linear body size growth curves, de Roos, 1997; and non-linear exploitation abilities, Lomnicki, 1988). This is because considering the mean and applying a non-linear function are not commutative, as was first proven by the mathematician Jensen at the beginning of the 20th century (Jensen, 1906). This mathematical property of non-linear functions, known as Jensen's inequality principle, states that for any non-linear function of a random variable the mean of the function does not equal the function of the mean (e.g., Ruel and Ayres, 1999; Appendix A).

Most demographic traits, however, translate non-linearly into per capita population growth rate and are themselves non-linear functions of more basic physiological traits. To illustrate this point consider the following example. Suppose that we have an organism with a seasonal life cycle. Our goal is to predict the number of individuals at the end of the growing season ( $N'$ ), which is a function of the starting number of individuals ( $N$ ), before reproduction occurs. This gives  $N' = p(t) \times N$  where  $p(t)$  denotes the probability of survival to the end of the growing season ( $t$ ). Survival probability can be described as follows:  $p(t) = \exp\left[-\int_0^t \mu(\tau) d\tau\right] = \exp[-M(t)]$ , where  $\mu(\tau)$  denotes an arbitrary time-varying mortality rate (e.g., within season variation in mortality rate as individuals increase in size or progress in their lifecycle). Thus, the integral of the mortality rate,  $M(t)$ , translates non-linearly into survival probability. Since the second derivative with respect to  $M(t)$  is always positive, increased variation in mortality rate (i.e., increased variance in  $M(t)$  among individuals, assuming no change in mean  $M(t)$ ) would result in an increased number of individuals at the end of the growing season (Appendix A). Note that the specific manner and causes of time-variation in mortality rate  $\mu(\tau)$  are implicitly described by  $M(t)$ , and thus irrelevant to the preceding argument concerning variation in  $M(t)$ ; such specific time-variation can be either random, monotonic, or other.

Mortality rate might, however, be influenced by a physiological trait such as body size ( $x$ ), i.e.,  $M(t)$  becomes  $M(x,t)$ .

Suppose that  $M(x,t)$  increases or decreases with body size as predicted by type I and type III survivorship curve, respectively (Deevey, 1947), or is a combination of both patterns (i.e., a U-shaped function) as suggested by theoretical (e.g., Kirkpatrick, 1984) and empirical studies (e.g., Caughley, 1966; van Straalen, 1985; DelGiudice et al., 2002). Let us also assume that there is little or no body size variation among individuals in the population and that the mean body size is approximately optimal with respect to mortality rate. In all three cases, increased body size variation should lead to increased mean mortality rate, resulting in a decreased final number of individuals. Body size variation also introduces variation in  $M(x,t)$ , however, this positive effect on mean survival is being overwhelmed by the negative effect through change in the mean  $M(x,t)$ . It is important to note that this is exactly the opposite of the previous result, which ignored the relationship between body size and mortality rate. This example shows that different levels of mechanistic detail can generate different predictions for the effect of variation among individuals on their population demography, and thus suggests that analytical generalizations may be limited.

We use here a computational simulator to examine the effect of body size variation among individual herbivores on their population demography and on the strength of plant–herbivore interactions. Specifically, we focus on a class of communities in which predators and herbivores complete their life cycle within one season and there are no overlapping generations (e.g., arthropod communities). Investigating such a system analytically would require a partial differential equation with several non-linear functions relating the  $p$ -state variable to  $i$ -state body size (Metz and Diekmann, 1986). Such an equation can most likely only be solved numerically, which requires specifying parameter values in addition to specifying the functions relating the  $i$ - and  $p$ -states. A simulation approach, on the other hand, has the advantage that some of the functions relating the  $i$ - and  $p$ -states emerge from simple rules of allometry or behavior applied to individuals (Schmitz, 2000; Grimm and Railsback, 2005).

### 1.1. Rationale

Answering questions about scaling from individual variation to community dynamics is currently a difficult task, using only the conventional top-down analytical modeling approach. This is because such an approach requires *a priori* specification of the mathematical functions that describe the interactions among individual herbivores, their resources, and their predators. By specifying the mathematical functions *a priori*, we imply that the causal links between individual variation and dynamics are completely understood. But we often do not know the form of the mathematical functions that link these organizational scales. Lacking such knowledge, one is typically forced to guess at the causal links and at the shape of the consequent model structure (Luttbeg and Schmitz, 2000; Schmitz, 2001).

To reduce the need for *a priori* guesswork, we begin by using a more bottom-up computational approach that enables us to identify the form of the functions through simulations. Specifically, in our computational approach, simulations are driven not by functions but by assigning rule sets to individuals in the

simulator at a fundamental level, i.e., physiology and behavior (Booth, 1997; Schmitz, 2000). These rules change as a function of body size and are literal translations of the behavior of organisms under field conditions. They thus allow us to emulate behavior observed under field conditions (Schmitz, 2000). Moreover, community dynamics emerge as a consequence of individuals acting according to these basic rules and are therefore more realistic.

In order to predict herbivore population dynamics and the consequent effects on plant abundance we had to know how herbivore survival and fitness are related to its body size. Since we could not predict these relationships *a priori*, we first conducted simulation experiments aimed at quantifying how survival and fitness are related to body size. We then varied the herbivore initial body size (HIB) distribution and tested the effects on its population demography and on the strength of plant–herbivore interactions. Finally, we explored to what extent we could predict these food web effects from HIB distribution in combination with survival and fitness curves. Specifically, we compared observed effects with predictions generated using only the trait mean and using both trait mean and variance. This allowed us to evaluate how the addition of variation influences prediction accuracy.

## 2. Methods

### 2.1. Computational simulator

We modeled the food web using Gecko, a spatially explicit individual-based model (IBM), which has been designed using the framework of complex adaptive systems (CAS) (Booth, 1997; Schmitz, 2000). The CAS framework explicitly addresses the traits of individuals and how these traits produce system responses (Railsback, 2001). The simplicity of the agents used in most CAS research, compared to real organisms, makes it easier to distinguish basic characteristics and themes of the studied system (Railsback, 2001). Thus, the CAS framework can help us overcome the system-level biases of ecology and the apparently overwhelming complexity of ecosystems, allowing us to focus on fundamental aspects of modeling population-level phenomena such as the emergent properties of individuals (Railsback, 2001). In other words, this new generation of IBMs can avoid many of the serious conceptual problems (e.g., inappropriate assumptions, mixing of individual- and population-level parameters) that typically characterized former IBMs (Railsback, 2001).

Gecko has a generic structure that can be applied to many different systems once the rules for a specific system have been identified empirically through lab experiments or field work (Kreft et al., 1998; Schmitz, 2000). We explored the dynamics of a food web consisting of two groups of plants, a herbivore that selects between the two plant groups providing different levels of nutrition and protection from predators, and a predator that preys on the herbivore. The structure of this Gecko version (see Appendix B) was inspired by recent empirical work investigating species interactions in a typical New England meadow food web consisting of spider predators, grasshopper herbivores, and herb and grass plant species (e.g., Beckerman et al., 1997). Thus, our intention is not to provide a

general explanation of the dynamics of all food webs. Rather, we focus on a class of food webs in which predators and herbivores complete their life cycle within one season and there are no overlapping generations.

Gecko simulations are driven not by functions but by assigning rule sets to individuals in the simulator at the fundamental levels of physiology and behavior (Booth, 1997; Schmitz, 2000). These rules change as a function of body size and they are literal translations of the behavior of organisms under field conditions. Individuals undergo un-gridded movement on a finite plane with reflecting boundaries. They are represented by spheres whose centers lie on this plane and they are free to move in two dimensions. An individual has a radius  $r$ , and accordingly a virtual volume  $4/3\pi r^3$  and an 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, to its biomass<sup>2/3</sup> (e.g., Peters, 1983; Calder, 1996; Belovsky, 1997). To stay alive, individuals must consume enough resources to meet metabolic requirements. Metabolic rate is proportional to biomass<sup>3/4</sup> (e.g., Schmidt-Nielsen, 1972; Peters, 1983; Calder, 1996). Because metabolic cost increases faster with individual biomass than resource intake rate, there are upper constraints to the maximum volume that an individual can reach. Individuals can overlap in space, allowing 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.

### 2.2. Simulation experiments

Scaling up from an individual trait to population and community dynamics should begin with linking this trait to demographic rates. We thus first conducted simulations to construct curves for herbivore survival,  $s$ , and fitness (i.e., per capita rate of change),  $w$ , as a function of its initial body size,  $x$ . We then conducted simulation experiments to generate dynamics under different scenarios of herbivore initial body size (HIB) variation. Finally, we evaluated the effect of trait variation on community dynamics by comparing observed food web effects with predictions generated using only the trait mean and both trait mean and variance.

### 2.3. Linking trait to demographic rates

We conducted short-term (one season) simulation experiments to quantify the link between HIB and demographic rates (i.e.,  $s$  and  $w$ ) using the no variation and maximum variation approach described below. For the no variation scenario, we generated 19 different populations of identical herbivores by systematically increasing HIB from 2.5 to 7.0 in increments of 0.25. We then ran simulations with an experimental setting including all three trophic levels (see Appendix B), and obtained 10 realizations for each of these 19 experimental food webs. We calculated the average survival and fitness for each of the 19 populations and constructed curves relating these demographic rates to HIB by linear interpolation.

For the maximum variation scenario, we generated a herbivore population in which all sizes were equally represented, i.e., uniform distribution ranging between 2.5 and 7. We then ran simulations with the same experimental setting as above, and obtained 10 realizations for this experimental food web. We tracked the survival and fitness of individuals in the same 19 size classes as above; however, in this case all size classes were present in the same population. In the same manner as above we constructed curves relating survival and fitness to HIB. The difference between these two sets of curves indicated to what extent frequency-dependence (i.e., effects of trait distribution on interaction strength) influences demographic effects of body size. Additionally, they were used to construct envelopes for mean survival and fitness given intermediate levels of HIB variation as described in the next section.

#### 2.4. Non-linearity versus frequency-dependence

To assess the importance of non-linearity versus frequency-dependence, we constructed envelopes for the effect of HIB variation on mean survival and fitness. The envelope is defined by the two extreme curves of no variation and maximal variation, which bound all other curves for intermediate levels of frequency-dependence. We generated herbivore populations in *Mathematica* 4.0 by drawing 1000 individuals from uniform HIB distributions, and calculated the survival ( $s_i$ ) and fitness ( $w_i$ ) of each individual  $i$  as function of its initial body size ( $x_i$ ) using the fitness and survival curves described above.

We calculated the population mean fitness,  $\bar{w} = \sum_{i=1}^{1000} w(x_i)/1000$ , and survival value  $\bar{s} = \sum_{i=1}^{1000} s(x_i)/1000$ , repeated this procedure for 22 populations with mean HIB 4.75 and standard deviation values between 0 and 1.3, and plotted the mean survival  $\bar{s}(\sigma_x)$  and fitness  $\bar{w}(\sigma_x)$  against the standard deviation of HIB,  $\sigma_x$ . These curves describe the effect of HIB variation on mean herbivore survival and fitness. We repeated this procedure for the fitness and survival curves ( $w(x)$  and  $s(x)$ ) from the no variation and the maximum variation scenarios; hence we constructed the curves  $\bar{s}(\sigma_x)$  and  $\bar{w}(\sigma_x)$  for both the no variation and the maximum variation scenarios.

The non-linearity of  $w(x)$  and  $s(x)$  makes mean population survival and fitness change with increasing HIB standard deviation,  $\sigma_x$ , as described by the curves  $\bar{s}(\sigma_x)$  and  $\bar{w}(\sigma_x)$ , while frequency-dependence makes mean herbivore fitness and survival travel from the no variation curves toward the maximum variation curve. These curves therefore describe envelopes for the herbivore mean survival and fitness for populations with mean HIB 4.75 and standard deviation ranging between 0 and 1.3. The widths of these envelopes indicate how important frequency-dependence is for the effect of HIB variation on mean fitness and survival (i.e., the wider the envelope the more important frequency-dependence).

#### 2.5. Predicting herbivore population demography

We conducted sequential simulation experiments for five seasons to test for the effect of trait variation on community dynamics. We generated five different populations of herbivores by systematically increasing HIB variation while keeping the mean HIB constant. At the beginning of each of the five

simulations 200 herbivores were drawn from a uniform distribution with a mean HIB of 4.75 and one of the following standard deviations: 0.000, 0.325, 0.650, 0.975 and 1.300. We then ran simulations with an experimental setting including all three trophic levels (for details see Appendix B). We assumed complete heritability of HIB, hence HIB distribution changed within a scenario from season to season. Since Gecko is a stochastic simulator, we obtained 10 realizations for each of the 5 experimental food webs and calculated the mean and standard error for the simulation outcome.

We first tested for the sensitivity of demographic rates to frequency-dependence by plotting how observed herbivore survival and fitness, from the first season of the five simulation scenarios, fall within the envelopes described above. The mean fitness and survival values from all other time steps (after the first season) do not necessarily fall within the envelopes since the mean and variance of HIB distribution, as well as the number of herbivores starting at each season, change over time and differ from the values used to construct the envelopes.

We then used the sequential HIB mean and variance ( $\bar{x}$ ,  $\sigma_x$ ) obtained during each of the four non-zero HIB variance scenarios (in total: 4 simulations  $\times$  4 time steps = 16 data points), to test whether the reconstructed fitness and survival curves,  $w(x)$  and  $s(x)$ , can accurately predict herbivore population dynamics by comparing observed herbivore population size with predictions generated in three different ways: (1) ignoring trait distribution, i.e., predicting the initial number of individuals in a given season ( $N'$ ) from the initial population size ( $N$ ) and the fitness of an average-sized individual ( $w(\bar{x})$ ) in the previous season using the following formula:  $N' = N \cdot w(\bar{x})$ . (2) Taking trait distribution into account, i.e.,  $N' = N \cdot \bar{w}(x)$  where  $\bar{w}(x)$  was calculated, as described earlier, by sampling 1000 HIB values ( $x$ ) from a uniform distribution with the same mean and variance as observed in the simulations to obtain a mean population effect using either the no variation or the maximum variation curve of  $w(x)$ . (3) Taking trait distribution into account but using a weighted average of the no variation and the maximum variation fitness functions:  $w(x_i) = (\sigma_{\text{obs}}/\sigma_{\text{MaxVar}}) \cdot w(x_i)_{\text{MaxVar}} + (1 - (\sigma_{\text{obs}}/\sigma_{\text{MaxVar}})) \cdot w(x_i)_{\text{NoVar}}$ .

#### 2.6. Predicting plant abundance

We tested if and to what extent effects of HIB distribution on herbivore survival influence final plant biomass. We first determined the effect of herbivore survival on final plant biomass during the five simulation experiments (5 simulation experiments  $\times$  5 time steps = 25 data points) by fitting parameters of the following regression model for each of the two plant types (i.e., safe and preferred):

$$\text{Biomass}_{\text{Plant}} = \beta_0 + \beta_1 \text{InitialNo.}_{\text{Herbivore}} + \beta_2 \text{Prop.Surviving}_{\text{Herbivore}}$$

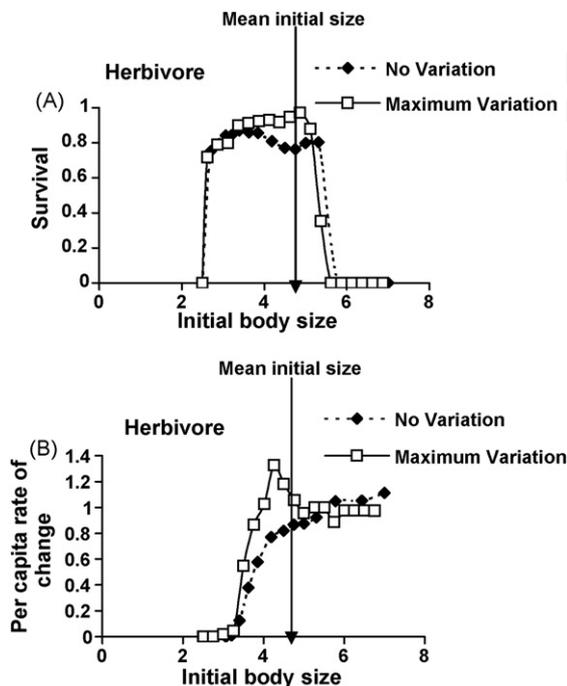
We next replaced the observed values of herbivore survival by survival estimates obtained in two different ways: (1) ignoring trait distribution, i.e., survival of an average-sized individual ( $s(\bar{x})$ ); and (2) taking trait distribution into account, i.e., calculation of  $\bar{s}(x)$ , as described earlier, by sampling 1000 HIB

values ( $x$ ) from a uniform distribution with the same mean and variance as observed in the simulations to obtain a mean population effect using either the no variation or maximum variation curve of  $s(x)$ .

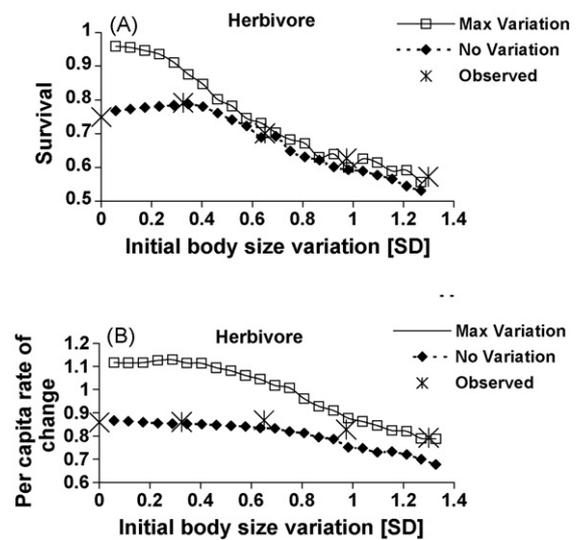
### 3. Results

#### 3.1. Linking trait to demographic rates

During both the no variation and the maximum variation scenarios survival of individuals at either extreme of the body size distribution was very low and thus generated hump-shaped survival curves (Fig. 1A). The no variation curve has two peaks (i.e., HIB equal to 3.4 and 5.1); the peak at smaller values of HIB is higher. The maximum variation curve peaks at HIB equal to 4.87. The relationship between HIB and fitness can be approximated using saturated curves (Fig. 1B). The no variation curve is a classical sigmoid, increasing rapidly at small HIBs until it reaches a maximum slope at HIB equal to 3.5. It then increases with HIB at a decreasing rate and eventually levels off. The maximum variation curve increases rapidly, peaks at HIB equal to 4.25, decreases rapidly and eventually levels off at HIB equal to 5.0. These estimated survival and fitness curves illustrate the utility of computer simulations such as Gecko, because there was no *a priori* way of anticipating their precise shapes.



**Fig. 1 – Body size-survival (A) and body size-fitness (B) curves estimated through simulations using two different experimental designs: (1) no variation—generating herbivore populations of varying initial body sizes but with no initial intra-specific body size variation; and (2) maximum variation—generating herbivore populations in which all body size classes are equally represented (uniform distribution).**



**Fig. 2 – Comparison of observed herbivore survival (A) and fitness (B) from the first season to predictions generated using initial body size distribution in combination with the no variation and the maximum variation body size-survival and body size-fitness curves.**

#### 3.2. Non-linearity versus frequency-dependence

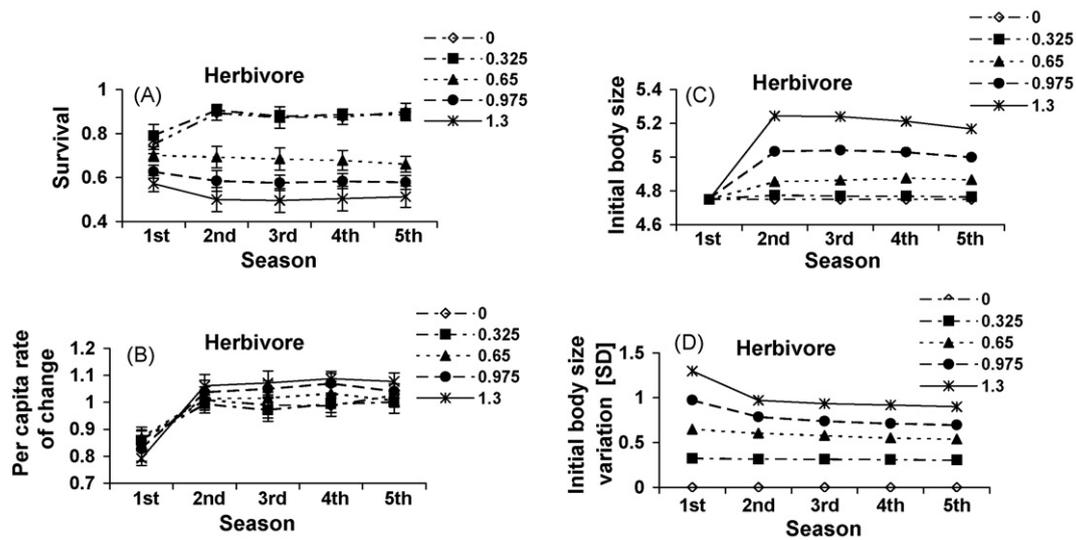
The herbivore fitness and survival envelopes (Fig. 2) indicate that frequency-dependence is more important for fitness than for survival. The results for the first season show that when variation was low it tended to have a positive effect on the proportion of surviving herbivores, but as variation increased this gave way to a strong negative effect on herbivore survival (Fig. 2A). A similar but weaker pattern was also detected for herbivore fitness (Fig. 2B).

As expected, when HIB variation was low the no variation curve could better predict herbivore survival and fitness (Fig. 2). However, as variation increased the predicted values generated using the no variation and the maximum variation curves converged (Fig. 2). Furthermore, differences between predicted curves generated using the no variation and maximum variation approaches were greater for fitness (Fig. 2B) than for survival (Fig. 2A). This means that our fitness curves were indeed sensitive to frequency-dependence.

#### 3.3. Observed food web effects

Our sequential simulation experiments showed that HIB variation had a negative effect on herbivore survival (Fig. 3A). When HIB variation was small (standard deviation of 0 and 0.325) there was an increase in survival over time, but when initial variation was high survival decreased over time. Across all variation treatments, most of the change in herbivore survival occurred between the first and the second season (Fig. 3A).

HIB variation had a negative effect on the per capita rate of change of herbivores during the first season (Fig. 3B). However, starting from the second season onward we observed a positive effect of variation on herbivore fitness. Additionally,



**Fig. 3** – The effects of HIB variation on herbivore survival (A), fitness (B), mean initial body size (C) and initial variation in body size (D) over a period of five simulated seasons.

across all variation treatments we detected an increase in the per capita rate of change over time with most of the change occurring between the first and the second season (Fig. 3B).

HIB variation had a positive effect on the herbivore mean body size (Fig. 3C). When initial variation was small there was almost no change in mean and variance over time (Fig. 3C and D). However, as initial variation increased we observed an increase in mean and a decrease in variance over time with most of the change occurring between the first and the second season (Fig. 3C and D). These patterns indicate that response to selection was stronger during the first season and are also consistent with a canalization process characteristic of scenarios where complete heritability is assumed. Notably, the loss of variability overtime, observed starting from the second season onward, was very slow (Fig. 3D).

Scaling up to the community-level, we found that increased HIB variation brought about an increase in the final biomass of both safe and preferred plants (Fig. 4A and B).

### 3.4. Predicting herbivore population demography

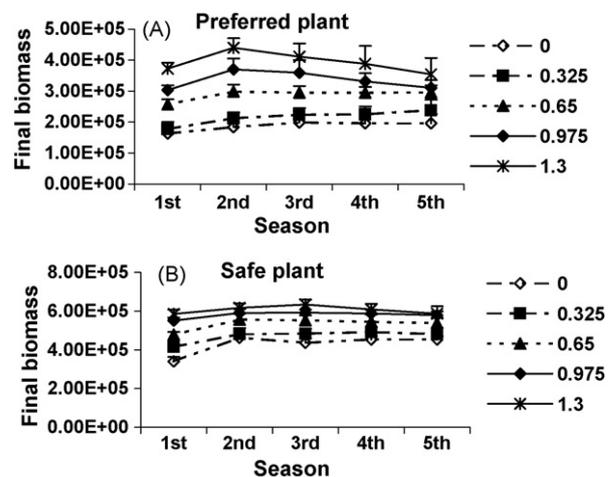
Using the no variation fitness curve and ignoring trait distribution almost always caused herbivore population dynamics to be underestimated (Fig. 5A). Using the maximum variation fitness curve and ignoring trait distribution generated data scattered above and under the one-to-one line (Fig. 5B), however, correlation between observed and predicted values was very low. In both cases, incorporating trait distribution increased the correlation between observed and predicted values, but deviations remained relatively large (Fig. 5C and D).

Examining our fitness curves we find that mean HIB is located where the maximum variation fitness curve is much higher than the no variation curve. Thus, at low and intermediate levels of variation, the maximum variation curve would always overestimate population size and the no variation curve would always underestimate the dynamics. In conclu-

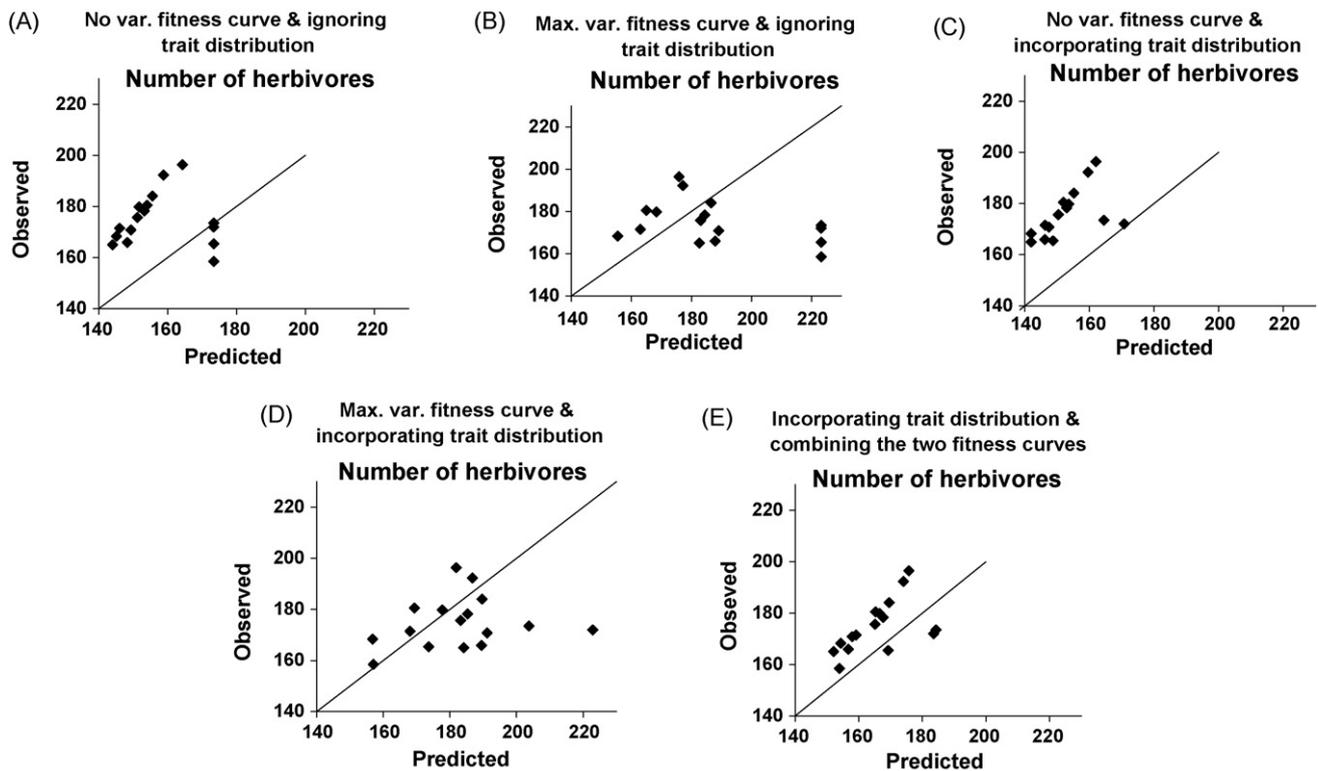
sion, generating accurate predictions for population dynamics in such a system where frequency-dependence changes constantly is almost impossible. Indeed, even when the weighted average between the two fitness curves was used the prediction improved only marginally (Fig. 5E).

### 3.5. Predicting plant abundance

Final (end of the season) biomass of safe and preferred plants was negatively correlated with herbivore survival:  $R^2=0.81$  and  $R^2=0.91$ , respectively. Similarly, we found a negative correlation between the final biomass of safe and preferred plants and initial herbivore population size ( $R^2=0.18$  and  $R^2=0.10$ , respectively). The multiple linear regressions produced the following coefficients:



**Fig. 4** – The effects of HIB variation on the final (end-of-growing-season) biomass of preferred (A) and safe (B) plants over a period of five simulated seasons.



**Fig. 5** – Comparison of the observed initial herbivore population size with predictions generated using the no variation (A and C) and maximum variation (B and D) body size–fitness curves when ignoring (A and B) and incorporating (C–E) initial herbivore body size distribution.

$$\text{Biomass}_{\text{SafePlant}} = 1.2 \times 10^6 - \text{InitialNo.}_{\text{Herbivore}} \times 2201 \\ - \text{Prop.Surviving}_{\text{Herbivore}} \times 4.5 \times 10^5$$

where  $R^2 = 0.81$ , and

$$\text{Biomass}_{\text{PreferredPlant}} = 1.0 \times 10^6 - \text{InitialNo.}_{\text{Herbivore}} \times 2054 \\ - \text{Prop.Surviving}_{\text{Herbivore}} \times 5.4 \times 10^5$$

where  $R^2 = 0.935$ .

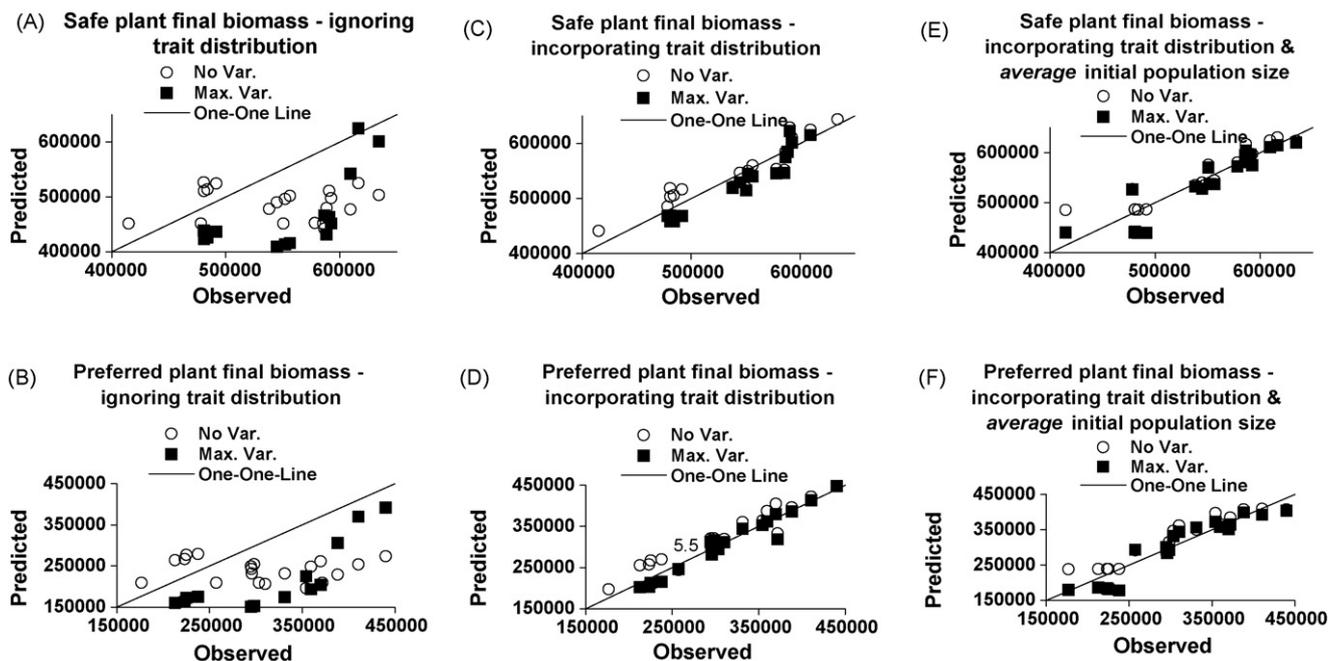
Using observed initial herbivore population sizes and herbivore survival estimated from the no variation or maximum variation curves by ignoring trait distribution resulted in an underestimation of final plant biomass (Fig. 6A and B). Incorporating trait variation yielded an accurate prediction of final plant biomass (Fig. 6C and D). Surprisingly, when the average initial herbivore population size was used instead of the observed values, the final plant biomass could still be accurately predicted (Fig. 6E and F).

#### 4. Discussion

We used a simulation model, designed to capture the structure of a typical New England meadow community consisting of spider predators, grasshopper herbivores, and herb and grass plant species (e.g., Beckerman et al., 1997), to explore the effects of initial body size variation among herbivores

on their population demography and on the strength of plant–herbivore interactions. We found that increased HIB variation decreases mean herbivore fitness and survival owing to the non-linear relationship between these demographic rates and HIB; however, it also increases mean fitness and survival owing to frequency-dependence. Frequency-dependence was more pronounced for herbivore fitness than for survival, complicating predictions for changes in herbivore population size between seasons. The effect of variation of HIB on mean survival owing to non-linearity was stronger than that of frequency-dependence, leading to a negative net effect of HIB variation on mean herbivore survival. Since the strength of plant–herbivore interactions depended strongly on herbivore survival, we could accurately predict the plant biomass at the end of each growing season from the distribution of HIB, even when we ignored the number of herbivores at the beginning of the season.

Our results oppose a fundamental assumption in classical community ecology theory, namely, that smaller-scale details such as the individual trait can be abstracted safely and that community dynamics can be simply characterized in terms of net changes in population densities. These findings are in accord with the growing sense among ecologists that an individual trait can stabilize population dynamics (Mangel and Roitberg, 1992), influence the strength of community-level interactions such as competition (Werner and Anholt, 1996) and predation (Beckerman et al., 1997), and be critical to the persistence of populations in the landscape (Lima and Zollner, 1996; Roitberg and Mangel, 1997).



**Fig. 6** – Comparison of the observed final biomass of safe (A, C and E) and preferred (B, D and F) plants with predictions generated using the no variation and maximum variation body size-survival curves when ignoring (A and B) and incorporating (C–F) initial herbivore body size distribution. The effect of initial herbivore population size on final plant biomass was tested by comparing observed effects to predictions generated using the values of initial herbivore population size estimated during the simulations (C and D), and to predictions generated using the arithmetic mean of these values (E and F).

Similarly, Uchmanski (1999, 2000) and Grimm and Uchmanski (2002) developed IBMs of consumer-resource dynamics, to investigate the effect of variability in initial body size on population stability and persistence. They showed that initial body size variation can enhance population stability and persistence, i.e., cause longer extinction times in comparison to homogenous populations. Scaling up to the community-level, de Roos and Persson (2002) constructed a size-structured IBM of predator-consumer-resource dynamics. They demonstrated how two general characteristics of individual consumer, namely, size- and food-dependent individual growth as well as a decrease in individual mortality with body size, can cause a compensatory growth (i.e., reduced reproductive success at low population densities, also known as Allee effect) at the predator population, and thus implying that catastrophic collapses of top predators may be an intrinsic property of many biological communities. In a more general context, these studies demonstrate that accounting for basic size-dependent ecological processes can induce qualitatively different community patterns, and thus suggesting that a food web theory, based on individual life history and individual variation, may differ substantially from classical and current theories in community ecology (de Roos and Persson, 2002).

Assessing the generality of our results requires an understanding of their mechanistic basis. The effect of HIB variation on mean fitness was strongly influenced by frequency-dependence. This frequency-dependence emerged because individuals with small and intermediate body sizes had higher

fitness when present in a population with a range of body sizes than in a population of identically sized individuals. At this point the mechanism causing this pattern – and hence its potential generality – is unclear. A possible explanation may be that as plant biomass increased with HIB variation, the competitively inferior size classes (i.e., simply owing to the properties of the allometric relationships between energy intake and expenditure; see also preceding paragraph) could survive better. Such relationship between minimum required resource density and body mass is known to drive complex population dynamics in fish populations (e.g., Persson et al., 1998).

In contrast, the negative effect of HIB variation on survival has a clear mechanistic explanation. This effect was driven by the fact that survival is highest for medium-sized individuals and decreases for small and large individuals owing to physiological constraints (i.e., a U-shaped mortality function). Therefore, increased HIB variation should decrease mean survival. This humped-shaped curve of survival as function of body size was not specified *a priori* but rather emerged from the rules used in the simulations. Specifically, according to general rules of allometry used in the simulations (e.g., Schmidt-Nielsen, 1972; Peters, 1983; Calder, 1996), small individuals have a relatively low capacity to digest and assimilate much of the food in their environment (e.g., Belovsky, 1997). They must therefore spend considerable effort in seeking high-quality food patches. Since such food patches tend to be comparatively rare, small individuals are subject to a higher starvation risk. Rules of allometry also suggest that

food intake and metabolic rate should be proportional to the surface area and the volume of an organism, respectively (e.g., Schmidt-Nielsen, 1972; Peters, 1983; Calder, 1996). Thus, although both rates are expected to increase with body size, the latter should increase faster. This means that there are upper physiological constraints on the maximum size that an individual can reach, and that very large individuals are also likely to be subject to a higher starvation risk. The fact that such humped-shaped survival curves are derived from basic principles implies that a U-shaped mortality function might be general across species and taxonomic groups. Indeed, early theoretical models in which body size rather than age was considered as the major determinant influencing demographic rates, suggested that a U-shaped mortality function, derived from a combination of different survivorship curves, may have a wider validity (e.g., Kirkpatrick, 1984). Moreover, the simple three-fold classification of survivorship curves (Deevey, 1947), has also been criticized by Caughley (1966) and van Straalen (1985) on the basis of empirical data (mammal and beetle species, respectively), also indicating a U-shaped mortality pattern.

In our simulations the negative effect of HIB variation on mean survival, mitigated by the hump-shaped survival-body size relationship, translated into a positive effect on plant biomass. Furthermore, because the between-season fluctuations in herbivore population size were relatively small (30% of initial population size), they could be abstracted safely. Thus, not only are trait-mediated effects potentially as important as those mediated by density, they can also control the entire community dynamics. However, at this point it is not clear whether trait variation in natural populations is strong enough to produce individuals with low survival. A field study on a food web with identical structure to the system analysed here that divided herbivores into three size classes demonstrated a decrease in survival only in the lowest size class but not in the highest (Ovadia and Schmitz, 2002). This study furthermore showed compensatory growth in the lowest size class—counteracting the effect of lower survival on plant biomass.

Our simulations showed that the envelopes for survival and fitness as a function of body size variation reveal important information about the predictability of the system. These envelopes could be constructed empirically in straightforward mesocosm experiments: herbivores are collected at the beginning of the season and grouped into body size classes. In one experiment individuals of the same size class are grouped together in mesocosms and their survival to the end of the season is recorded. In a second experiment mesocosms containing the entire range of size classes are created and the survival of individuals in each size class is recorded.

Our results suggest directions not only for empirical studies but also for further theoretical investigation. Frequency-dependence sets limits to simulations or experimental studies since it is not feasible to explore all patterns of trait variation within a population. Understanding effects of variation in physiological traits on mean demographic rates that are driven by frequency-dependence therefore requires analytical approximations. Finally, a complete description of the interplay between individual variation and community dynamics requires not only an understanding of how individual varia-

tion translates into population-level rate parameters but also of the mechanisms creating and maintaining individual variation in physiological traits such as body size (e.g., Uchmanski, 1985; Kimmel, 1986; Pfister and Stevens, 2003; Peacor and Pfister, 2006). To conclude, in classical as well as more recent models, community dynamics can be predicted given population size or a combination of population size and trait. Here we propose using trait distribution as a major determinant for predicting community dynamics. Doing so will require: (1) experimentally studying the link between life history traits and demographic rates; (2) designing experiments to test for the effects of trait distribution on community dynamics; (3) extending the traditional models that are exclusively based on numerical effects and/or a combination of density- and trait-mediated effects to incorporate mechanisms that shape the distributions of dynamically relevant traits.

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## Appendix A. Jensen's inequality

Jensen's inequality states that for any real continuous function  $f(x)$  of a random variable  $x$ , the inequality  $\sum f(x_i)/n > f(\sum x_i/n)$  holds if  $f(x)$  is concave-up (i.e., second derivative is positive). The inequality is contrary if  $f(x)$  is concave-down (i.e., second derivative is negative), and is strict unless  $x_1 = x_2 = \dots = x_n$  (i.e., all  $x$ -values are the same). To illustrate the application of Jensen's inequality to the problem of individual variation in ecological dynamics consider a function  $g(x)$  that relates population demography to an underlying trait distribution. The effect of mean ( $\mu$ ) and variance ( $\sigma_x^2$ ) in trait value can then be approximated using a second-order Taylor series expansion of  $g(x)$  around the mean-value  $\mu$ . We can then arrive at the following formula for the expected value of  $g(x)$ :  $E(g(x)) \cong g(\mu) + \sigma_x^2 \cdot g''(\mu)/2$ , also known as the variance discounting formula in evolutionary ecology (Lacey et al., 1983; Real and Ellner, 1992). (Note that the expected value notation  $E(\cdot)$  refers to arithmetic mean, rather than geometric or harmonic.) This equation states that the difference between the mean of the function ( $E(g(x))$ ) and the function of the mean ( $g(\mu)$ ) depends on the second derivative of the function ( $g''(\mu)$ ) and on the trait variance ( $\sigma_x^2$ ). For a linear relationship ( $g''(\mu) = 0$ ) the mean of the function is equal to the function of the mean. Thus, in this case, it should be safe to use the mean trait value to predict population demography. However, whenever the function is concave in the vicinity of the mean-value  $\mu$ , i.e.,  $g''(\mu)$  is either positive or negative, ignoring trait variation would result in underestimation (concave-up;  $g''(\mu) > 0$ ) or overestimation (concave-down;  $g''(\mu) < 0$ ) of population demography.

## Appendix B. Gecko structure

### B.1. Plant rules

Plants absorb nutrients directly from the plane and compete for nutrients. Local resource uptake is proportional to an individual's resource gathering capabilities, i.e., its area. Large individuals have a competitive advantage because they can deplete the resource pool at a faster rate than smaller individuals. Competition causes anything from reductions in individual body size growth to 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.

Plants 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:

$$\text{distance} = (\text{parent radius} + \text{offspring radius}) \times e^x,$$

where  $x$  denotes a random variable with uniform distribution on the unit interval  $[0,1]$ . This guarantees that parent and offspring never overlap in space immediately after reproduction. Offspring are also placed in a random direction away from their parent.

The two plant species representing the primary producers in our food chain were identical in terms of all parameters used to estimate their resource intake rate, growth rate, reproduction rate, etc. They differed only in terms of the herbivore's perspective. One plant species was highly nutritious and thus termed "preferred" plant. The second, "safe" plant was less nutritious but represented a refuge from predation. By creating this type of community structure we introduced the classical trade-off between food and safety for the herbivores.

### B.2. Herbivore rules

Herbivores have perception and intent that stimulates movement on the landscape, which is effectively a correlated random walk with reflecting boundary conditions. They actively search for resources (plants) within a designated search path width that scales to their body size radius. The distance that herbivores move at each time step is equal to their body size radius. Directional movement is steered by a "veer" function, i.e., they move forward in the general direction they face plus or minus a random veer of no more  $\pi/2$  radians ( $90^\circ$ ) left or right of their current direction. When feeding, 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. 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. Plants, however, are never completely consumed or directly killed by herbivores.

Herbivores have a predator detection radius that is a multiple of their body size radius and they are designed to respond adaptively to the presence of predators. When a predator enters the herbivore's detection radius, a predation threat is signaled and the herbivore freezes for one time step. If in the next time step the predator is again detected, the herbivore will make an attempt to evade the predator by moving away from the oncoming predator. Herbivores will only retreat to safe plants when confronted by a predation threat. In this scenario, smaller (younger) herbivores will have smaller detection radii and therefore they will have less time to evade predators than do larger herbivores, placing them at greater risk. 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.

Herbivores undergo asexual reproduction when their size exceeds a minimum breeding volume. However, since we assumed non-overlapping generations, we kept the offspring non-active (eggs) until the end of the season. The initial body size radius of each offspring, when introduced in the next season, is copied from its parent (i.e., complete heritability).

### 4.1. Predator rules

Predators use an active hunting mode. They have an attack radius that enables them to detect and then actively hunt prey. This attack radius is a multiple of their body size radius. They search randomly until a prey item is detected within the attack radius and they then move directly toward that prey item. A predation event occurs when there is contact (or an overlap) between the prey and the predator. Here the biased random walk of the predator is driven simply by prey detection and opportunity for capture. For simplicity, we assumed that predators do not undergo population dynamics. Rather, they were treated as an environmental component of the plant-herbivore interaction by simply having a constant density of predators in each season.

### 4.2. Time and seasonality

In Gecko, the focus of time is on feeding, so a time step is equal to the portion of a day taken up by a feeding period (e.g., one to several hours). In our simulations, a day is comprised of ten feeding periods. The landscape produces resources incrementally at each time step. Within each time step, resources are consumed in discrete units by plants and animals.

We incorporated seasonality into the computational model by dividing a season into a growing period of 2200 time steps (i.e., 10 "hours" per day  $\times$  220 days) and a dormant period of one 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 220-day growing season germinate and grow; seeds produced at the end of the season remain dormant until the next grow-

ing period. Due to physiological constraints, however, plants tend to grow vegetatively (increase in 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 subsequent growing period.

Herbivores and predators are introduced into the environment after 100 days (1000 time steps) in each season. A similar delay characterizes arthropod communities in temperate regions. In the simulations, herbivores must accrue enough resources to grow and they can only reproduce as adults (i.e., they must reach a critical body size before they can reproduce). 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 reproduce several times 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 reproduction occurred (eggs were laid) in the previous growing season.

#### 4.3. Energy flow and nutrient recycling

Using rates for resource-biomass conversion reported by Hairston and Hairston (1993), we 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. 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.

#### 4.4. Stochasticity

Stochasticity enters the simulations in several ways. First, it arises from the initial random seeding of organisms onto the landscape. 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, their body size 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 a random distance away from their parents (distribution is described in the plant rules section).

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