

## PLANT–ANIMAL INTERACTIONS IN RANDOM ENVIRONMENTS: HABITAT-STAGE ELASTICITY, SEED PREDATORS, AND HURRICANES

CAROL C. HORVITZ,<sup>1,4</sup> SHRIPAD TULJAPURKAR,<sup>2</sup> AND JOHN B. PASCARELLA<sup>3</sup>

<sup>1</sup>Department of Biology, University of Miami, Coral Gables, Florida 33124-0421 USA

<sup>2</sup>Biological Sciences, Stanford University, Stanford, California 94305 USA

<sup>3</sup>Department of Biology, Valdosta State University, Valdosta, Georgia 31698 USA

**Abstract.** When environments change stochastically, the question arises how to evaluate the effects of a plant–animal interaction on the fitness of the plant, where plant fitness is measured by the stochastic growth rate. We develop the concept of habitat-stage elasticity,  $E_{\beta}^S$ , which gives the proportional sensitivity of the stochastic growth rate to perturbations of stage transition rates in each state ( $\beta$ ) of the habitat. We employ it to understand why a specialist gall-making seed predator has relatively low impact on the fitness of a subtropical shrub. The plant lives in a forest characterized by patchy, recurrent disturbances caused by hurricanes. Both predation rate and plant demography vary with canopy openness. In the most closed-canopy state, the seed predator destroys 90% of the fruits, and demographic quality, the dominant eigenvalue of that state's matrix, is low, while in the most open-canopy state, predation is negligible and demographic quality high. The seed predator is locally extirpated by strong hurricanes, recolonization taking several years.

The effect of the predator on the stochastic growth rate is negligible at both low and high hurricane frequency. Its effect peaks (6%) at an intermediate hurricane frequency. The stochastic growth rate varies in its sensitivity to the predator in different states of the habitat due to a product of two factors: the frequency of the state in the environment and the contribution of fecundity to its elasticity. The latter factor encapsulates the expected sequence of future states of the habitat. In our system, the contribution of fecundity to elasticity of the darkest state increases with hurricane frequency, even though the probability of encountering that state decreases, because today's dark habitats are more likely to become lighter ones. The contribution of fecundity to the two lightest states does not vary with hurricane frequency. In contrast, its contribution in intermediate states at intermediate hurricane frequencies is most dynamic, since uncolonized states may become colonized states and insensitive states may become sensitive states. The effects of an animal on plant fitness is determined by the disturbance regime in addition to its impact on vital rates in each environmental state.

**Key words:** *Ardisia; effects of animals on plant fitness; environment-specific elasticity; gall-making moths; habitat elasticity; Periploca; stochastic growth rate; stochastic sequence.*

### INTRODUCTION

In this paper we examine the demographic impacts of animals on plants in random environments. Plant–animal interactions and their outcomes exhibit marked variability in different states of the environment (Horvitz and Schemske 1990, Thompson 1999, Herrera et al. 2002). When environments change stochastically, how can one evaluate the effects of a given interaction, whose outcome also varies, on the fitness of the plant, as measured by the stochastic growth rate?

For example, there has been considerable debate about whether herbivores and seed predators can substantially alter population dynamics of long-lived perennial plants and which are the critical stages of impact (Crawley 1989, Strauss and Agrawal 1999). Early

studies quantified the effects on single fitness components or short-term parameters, but recent studies have been more concerned with long-term effects. Several studies have combined observational and experimental data from a few years with a variety of modeling approaches to simulate long-term effects on individual plants and populations, but only a few emphasize the population growth rate or the stochastic growth rate as the parameter for measuring population success (e.g., Bastrante et al. 1995, Ehrlen 1995, 2003). Ehrlen (2003) emphasized an LTRE (life table response experiment) analysis (sensu Caswell [2001]) of the effects of herbivores on population growth rate. The parameter that contributed most to the difference in population growth between treatments (with and without herbivores) was a parameter that was only weakly affected by herbivores, but had high sensitivity. There was little interannual variation in Ehrlen's (1995) study system and the stochastic growth rate did not provide distinct insights from single-matrix analyses. In contrast, Bas-

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<sup>4</sup> E-mail: carolhorvitz@miami.edu

trante et al.'s (1995) study was characterized by strong temporal variation in demography. This study used the stochastic growth rate to determine how many poor years could be tolerated by a plant under different grazing and germination regimes. There was an interaction between herbivory and environmental variability in their effects on plant fitness.

These two studies together set the stage for the current paper: demographic sensitivity and environmental variability may both be important in trying to understand the effects of animals on plants. In other studies concerned with the effects of herbivores and seed predators on plant populations, several measures of plant population success have been used, including lifetime reproductive success of individuals (Doak 1992), size attained by reproductive individuals (Doak 1992), abundance of adult plants and of seeds after a set number of years (Maron and Gardner 2000), density of juvenile plants (Maron et al. 2002), cumulative seed production (Doak 1992), and cumulative seedling recruitment (Maron et al. 2002). These studies are somewhat less comparable because of the diverse currencies employed. It is not our intention to review this literature; instead we propose that the continuing debate about whether herbivores and seed predators can substantially alter population dynamics of long-lived perennial plants may be illuminated by seeking consensus on an appropriate fitness measure in variable environments and its sensitivity analysis.

We propose an approach that is applicable to many long-lived plants and that allows for variation in plant demography and in a plant–animal interaction. Its application to other systems may aid in our search for patterns and generalities about whether and when plant–animal interactions are likely to have strong impacts on plant fitness. We analyze the dynamics of structured populations modeled by population projection matrices. Temporal variation is described by associating a distinct projection matrix with each of several distinct environments, such as those arising over time following a disturbance (Cohen 1977, Horvitz and Schemske 1986, Tuljapurkar 1997). We develop the concept of habitat-stage elasticity to investigate how the stochastic growth rate,  $\lambda_s$ , differs in its sensitivity to interactions that occur in different states of the habitat.

We apply this concept to understand how a specialist seed predator impacts the fitness of a plant living in an environment of patchy, recurrent disturbances caused by hurricanes. We further analyze how changing the disturbance regime alters the fitness consequences of the plant–animal interaction. Plant demography (Pascarella and Horvitz 1998, Tuljapurkar et al. 2003) and the impact of the seed predator (a moth) on seed production (Pascarella 1998) were estimated from empirical data. In this paper, we employ plausible scenarios of moth population dynamics and compare plant population dynamics in an environment that is moth-

free to environments created by these scenarios. We show that the effect of the animal on seed production in the most frequent state of the habitat is not predictive of its effect on the stochastic growth rate. Further, our analysis shows that the expected sequence of future states of the habitat influence the effect of the interaction in a given state of the habitat.

In our study system, the most frequent state of the random environment is dark forest, in which gross plant fecundity is low and moth attack rate is high. A field ecologist who measured the effects of the moths across a series of patches in southern Florida given the current pattern of hurricanes, would likely conclude that, on average, the moth is a major threat to plants, since it kills nearly 90% of the already scarce fruits. Does this picture correctly depict the effects of the moth on plant fitness? We show that the answer to this question is “no.” The effects of an animal on a fitness component within a single state of the environment (even if that is a frequently encountered state) is not equivalent to its effects on the stochastic growth rate. This is because the stochastic growth rate is determined by not only the frequency, but also the sequence of habitat states and because sequence does matter.

Specifically, we address three questions: (1) How does the moth affect the stochastic growth rate,  $\lambda_s$ , for plausible scenarios of moth recolonization dynamics? (2) How does the frequency of hurricanes alter the effects of the moth? (3) How does habitat-stage elasticity help us to understand the effects of moths and hurricanes on stochastic population dynamics?

## MATERIALS AND METHODS

### *The plant, the moth, and hurricanes*

The plant species is an understory shrub (*Ardisia escallonioides* Schlecht. & Cham. [Myrsinaceae]) in a forest landscape where canopy-gap dynamics is driven by hurricanes (Pascarella 1995, Pascarella and Horvitz 1998, Tuljapurkar et al. 2003). The moth is *Periploca* sp. (Cosmopterigidae), a specialized gall maker on the flowers of *A. escallonioides* (Pascarella 1998). The vital rates of the plant vary with canopy openness. Each of seven distinct habitat states, along a gradient of canopy openness from very light to very dark, is characterized by a distinct population projection matrix for the plant. Gross fruit production ranges from very high, >3000 fruits per large-reproductive plant per year, in the most open-canopy habitat (habitat 1) to very low, <25 fruits per large reproductive per year, in the closed-canopy habitat (habitat 7). Gross fruit production in each of the intermediate habitats ( $857 \pm 208$  fruits per large reproductive plant [mean  $\pm$  SD]) is less than one third of the open-canopy value (Fig. 1A). Each fruit produces a single seed. Gross fruit (and seed) production is given by adding the number of fruits attacked by moths (“gall fruits”; see Plate 1) to the number of fruits not attacked. Attacked fruits do not produce seeds, and the attack

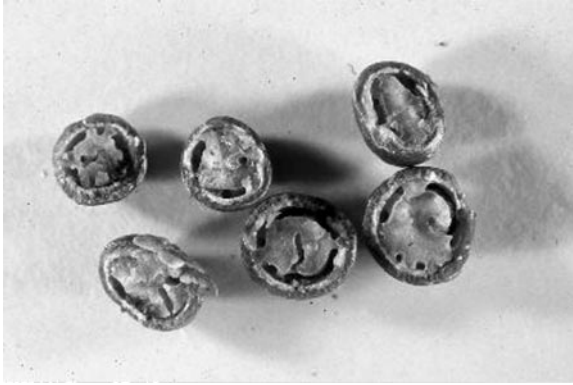


PLATE 1. *Ardisia escallonioides* "gall-fruits." These are "fruits" (which remain green, never ripen and never produce mature seeds) that result from flowers in which the gall-making specialist moth, *Periploca*, lays its eggs; the larvae develop in these galls. Photo credit: J. B. Pascarella.

rate of the moth varies among habitats (Pascarella 1998).

We counted the moths at the larval stage, when each one forms a gall. Moths lay eggs in flowers in the fall and overwinter as larvae in the "gall fruits," which do not ripen in the spring, but remain green. There is one larva per gall and the galls are readily identified, counted, and distinguished from unattacked fruits. Thus counting gall fruits and unattacked fruits provides an estimate of moth abundance, attack rate, and gross fruit production. Larvae leave the galls during the late summer to pupate and remain in the soil for 4–5 weeks. Adults emerge coincident with the flowering peak in the fall, needing flowers on which to lay their eggs. If there are no flowers available (which happens in forest patches hit by strong hurricanes that strip all leaves and flowers from plants), they have nowhere to lay eggs, and the moth population becomes locally (temporarily) extinct (Pascarella 1998). For this reason, moths were absent from state 1, the very-open-canopy habitat.

In previous analyses of population dynamics of this species (Pascarella and Horvitz 1998, Tuljapurkar et al. 2003) we used counts of unattacked fruits to obtain fecundity estimates. In this paper, we use counts of gross seed production and estimates of attack rates to obtain fecundity estimates under different scenarios of the plant–animal interaction. We consider one scenario (hereafter termed "no moths") in which moths are absent from the landscape in which gross fruit production (Fig. 1A) estimates fecundity. Empirical data on moth occurrence and recolonization over several years in southern Florida (USA) following a hurricane (Pascarella 1998) showed that in the lightest state of the habitat (state 1), moths were virtually absent (here we assume an attack rate of 0.00001 of fruits), and moths reached maximum attack rate (0.8926 of fruits) in the darkest state of the habitat (state 7). There is a three-

fold increase in moth attack rate between successive states of the environment (from open to closed canopy). We study scenarios created using five values of the moth recolonization rate,  $r$ , the rate at which moth abundance increases between successive states of the habitat. Values of  $r$  ranged from 2.6 to 4.2; the highest generates what we call the "rapid-recolonization" scenario (see Appendix A).

Fecundities in each state of the habitat for each scenario were calculated by applying the attack rates generated for each scenario to the gross fecundity estimates. To frame the possible outcomes, we focus on the no-moths and the rapid-recolonization ( $r = 4.2$ ) scenarios. In each scenario, the dominant eigenvalue of each of the seven habitat-specific matrices measures the demographic quality of each habitat state: how the population would do if the conditions encapsulated in the vital rates were to remain unchanged (Caswell 2001). By this measure, for both scenarios, the best habitat is the open canopy, state 1, and the worst is the closed canopy, state 7 (Fig. 1B). Also, adding moths to the system appears to have its largest impact on habitat quality in states 4, 5, and 6, and negligible effects in states 1, 2, 3, and 7 (Fig. 1B). For example, moths reduce the quality of habitat 5 by 25.5%, but they only reduce the quality of habitat 7 by 2.4%.

#### Brief description of the model of population dynamics

The model of population dynamics for the plant is detailed in Tuljapurkar et al. (2003). Here we outline

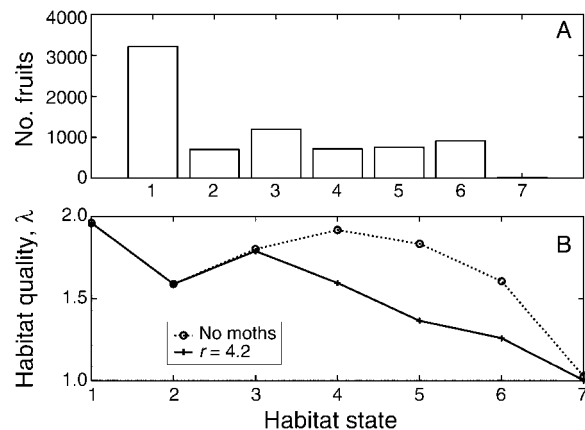


FIG. 1. Habitat states with respect to number of fruits produced and habitat quality. (A) Gross number of fruits (seeds) produced per year per large reproductive plant in each state of the habitat, estimated by the sum of gall "fruits" and unattacked fruits. Habitats range from a very light environment with an open canopy, state 1, to very shady environment with a closed canopy, state 7. In intermediate states 2–6, plants produced a mean ( $\pm$  SD) of  $857.3 \pm 208.4$  fruits, averaged over the  $N = 5$  intermediate states of the habitat. (B) Demographic quality of each state of the habitat, estimated by the dominant eigenvalue of the population projection matrix associated with each state of the habitat, in an ideal world of no moths and in a world where moth abundance increases rapidly: moth recolonization rate  $r = 4.2$ .

the main features of the model that are relevant for this paper. The matrix element  $A_{i,j,\beta}$  is the rate at which individuals in stage  $j$  produce individuals in stage  $i$  over one time step whenever the population is in habitat state  $\beta$ . The top row of the matrix represents the fecundities. The probability that the habitat state changes from state  $\beta$  to state  $\alpha$  over one time step is written  $c_{\alpha,\beta}$ , and is an element of a Markov transition matrix  $\mathbf{c}$ . This matrix contains the probability rules used to generate a sequence of habitat states over time. Its dominant right eigenvector,  $\mathbf{f}^*$ , with elements  $f_{\beta}^*$ , gives the stationary probabilities of observing each state of the habitat. The population numbers by stage at time  $t$  are enumerated in vector  $\mathbf{N}(t)$ . The population is governed between  $t - 1$  and  $t$  by a random vital-rate matrix  $\mathbf{X}(t)$  that takes on values determined by the habitat state at time  $t - 1$ , and

$$\mathbf{N}(t) = \mathbf{X}(t) \mathbf{N}(t - 1). \quad (1)$$

The total population  $P(t)$  at time  $t$  is the sum of the elements of  $\mathbf{N}(t)$  and the stochastic growth rate,  $\lambda_s$ , is obtained from the following equation:

$$\log \lambda_s = \lim_{t \rightarrow \infty} (1/t) \log [P(t)/P(0)]. \quad (2)$$

We obtained stochastic growth rates from numerical simulations (Caswell 2001, Tuljapurkar et al. 2003; note that these authors follow different conventions for naming the matrices [see Appendix B to clarify the relation between their equations describing population growth in stochastic environments]). To address the fitness consequences of the plant–animal interaction under distinct disturbance regimes, we obtained a stochastic growth rate for each of the six scenarios of moth recolonization dynamics for each of 40 hurricane frequencies. For any given hurricane frequency, comparing the stochastic growth rate in the scenario of no moths to the stochastic growth rate in a scenario of rapid-recolonization constitutes a direct measure of effect of moths on plant fitness. Similarly, for any given moth scenario, comparing the stochastic growth rate across hurricane frequencies constitutes a measure of how disturbance regime impacts plant fitness. The interaction of moths and disturbance regime on fitness is understood by examining the effects of moths at several different hurricane frequencies.

From the historical record, Pascarella and Horvitz (1998) calculated the probability of a hurricane at the study site in any given year as  $P(\text{hur}) = 0.081$  and from this, combined with other data, estimated a habitat transition matrix. In this paper we follow Tuljapurkar et al. (2003) and investigate a range of hurricane frequencies lower and higher than historical. Disturbance frequency may vary in different geographical locations or because of climate change, and our results indicate the consequences of such variation. At the historical hurricane frequency, the random environment is dominated by the darkest habitat, 7, but at 10 times this

frequency, the random environment is dominated by the lightest habitat, 1 (Fig. 2C). The habitat states of intermediate canopy openness do not dominate the scene at any hurricane frequency, although for each one, there is a particular frequency of peak occurrence (see Appendix C).

#### *Stochastic elasticity and habitat-stage elasticity*

Elasticities are a tool for understanding the effects of moths on plant fitness. Stochastic elasticity is an analogue of deterministic elasticity. The  $ij^{\text{th}}$  element of  $E^s$ , written  $e_{ij}$ , is the proportional change in  $\lambda_s$  produced by a 1% change in the  $ij^{\text{th}}$  population matrix element in every state of the habitat. In Tuljapurkar et al. (2003: 494), we point out that  $\lambda_s$  will respond to perturbations of life-history rates in each state of the habitat differently. We describe this by matrices of habitat-stage elasticities,  $E_{\beta}^s$ , where  $\beta$  is a particular state of the habitat. An entry,  $e_{i,j,\beta}$ , in each matrix, addresses the issue of how perturbing the  $ij^{\text{th}}$  life-history transition when a population is in state  $\beta$  affects the stochastic growth rate. It gives the potential stage and habitat-specific selection on a trait that influences a given life-history rate in a particular state of the habitat. With respect to moths, their impact on plant population dynamics will depend upon the state of the habitat they colonize.

For seven hurricane frequencies (see Appendix C), we estimated habitat-stage elasticities from numerical simulations of at least 20 000 time steps (100 000 time steps were used when needed for inclusion of rare habitat states), storing the sequences of habitat states, population structure vectors,  $\mathbf{u}(t)$ 's, reproductive value vectors,  $\mathbf{v}(t)$ 's, population projection matrices,  $\mathbf{X}(t)$ 's, and one-time-step growth rates,  $\lambda(t)$ 's, generated by the stochastic process (Tuljapurkar et al. 2003). Storing these sequences allows us to pick out occurrences of a particular habitat state in the sequence and to analyze the behavior of the system contingent on being in this state.

For example, suppose that vital rates depend on canopy openness, and canopy openness changes randomly, and that we will perturb vital rates only when there is a very open canopy. Formally, let  $F(t)$  indicate the random state of the environment at time  $t$ , and let  $\mathcal{A}$  indicate a set of values of the environment. We now make a perturbation of vital rates from  $\mathbf{X}$  to  $(\mathbf{X} + \delta\mathbf{C})$  only when  $F(t) \in \mathcal{A}$ . Define the indicator function

$$I(t, \mathcal{A}) = \begin{cases} 1 & \text{if } F(t) \in \mathcal{A} \\ 0 & \text{else.} \end{cases} \quad (3)$$

Then we define a habitat-stage elasticity matrix

$$D_{ij}(\mathcal{A}) = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^{T-1} \frac{v_i(t) C_{ij}(t) I(t, \mathcal{A}) u_j(t-1)}{\lambda(t) [\mathbf{v}(t), \mathbf{u}(t)]}. \quad (4)$$

Our computations use MATLAB code (MATLAB 2004).

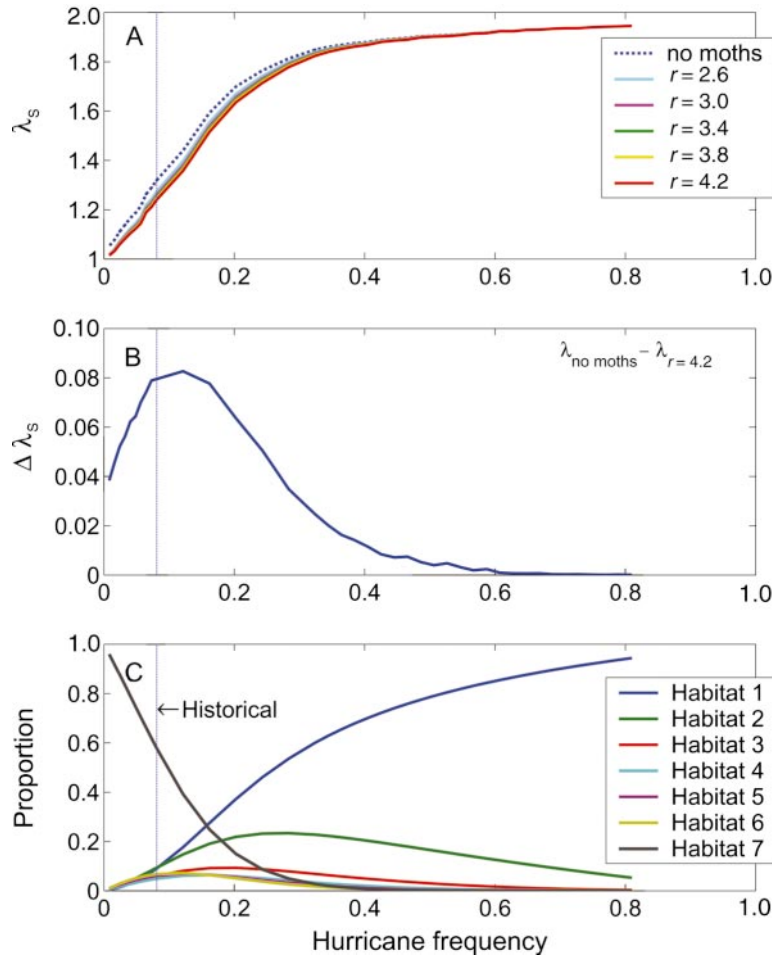


FIG. 2. Effects of hurricane frequency on (A) plant fitness, measured by the stochastic growth rate,  $\lambda_s$ , for each of six moth scenarios of moth-recolonization dynamics ( $r$  = the moth recolonization rate); (B) the difference between fitness in an ideal world of no moths and fitness in a world where moth abundance increases rapidly,  $r = 4.2$ ; and (C) the statistically stationary frequency of habitat states. Forty hurricane frequencies were investigated. The historical hurricane frequency is indicated by a vertical line.

This protocol yields a set of habitat-stage elasticity matrices,  $E_{\beta}^S$ , one for each state of the habitat. In our case, there are seven states of the habitat and thus seven  $E_{\beta}^S$ 's.

#### Components of habitat-stage elasticity

The stochastic elasticity,  $E^S$ , is the sum over habitats of the habitat-stage elasticities,  $E_{\beta}^S$ . Previous work has established that the sum over  $i$  and  $j$  of the elements  $e_{ij}$  of  $E^S$  equals 1 (Caswell 2001). Here we point out that a similar sum over  $i$  and  $j$  of  $e_{ij,\beta}$  for each  $\beta$  equals the stationary probability of observing habitat  $\beta$ ,  $f_{\beta}^*$ . This quantity can also be thought of as habitat elasticity, because it answers the question how the stochastic growth rate would change if all the life-history rates in habitat state  $\beta$  were perturbed by 1% each time the state occurs. The sum of  $f_{\beta}^*$  over  $\beta$  equals 1. We also note that a particular habitat-specific elasticity,  $e_{i,j,\beta}$ , is not simply the product of  $f_{\beta}^*$  with the stage elasticity,

$e_{ij}$ . Indeed the difference between these quantities is key.

The magnitude of each  $e_{i,j,\beta}$  (or any summation of them) is the product of two components: the habitat elasticity and the relative importance of the transition (or the summation of several transitions) to the habitat elasticity. The sum of all the  $e_{i,j,\beta}$  for all  $i$  and  $j$  for a given  $\beta$  provides a measure of the first component, equivalently given by  $f_{\beta}^*$ . The second component is given by dividing each  $e_{i,j,\beta}$  by this sum. The result is the proportional contribution of stage transitions to habitat elasticity. This parameter allows comparison of the shape of elasticity across states of the habitat independent of their frequency.

With respect to our focal issue, the effects of a seed predator on fitness, we were especially interested in habitat-stage fecundity elasticities and the proportional contribution of fecundity to habitat elasticity. We summed elasticities corresponding to fecundity tran-

sitions, the top row, ( $i = 1$ ). To see which kinds of transitions were important when fecundity was not, we also summed elasticities corresponding to regression (above the diagonal but below the top row), stasis (along the diagonal) and growth (below it).

RESULTS

*Effects of moths on the stochastic growth rate,  $\lambda_s$*

The effects of moths on plant fitness are subtle relative to the dramatic effects of hurricane frequency (Fig. 2A). Plant fitness is highest in the persistently high-light environment created by very frequent hurricanes. For any given hurricane frequency, plant fitness decreases as moth recolonization,  $r$ , increases, the magnitude of this effect depending upon hurricane frequency. The fitness difference between the no-moths and the rapid-recolonization scenarios ranges from 0 at very high hurricane frequency to a peak of 0.0827 at  $P(\text{hur}) = 0.1215$ , a bit higher than historical (Fig. 2B). At this peak, the proportional effect of moths on plant fitness is about 5.7% reduction in fitness relative to the no-moths scenario (calculated as  $(\lambda_{\text{no moths}} - \lambda_{\text{rapid recolonization}})/\lambda_{\text{no moths}}$ ). At the historical hurricane frequency ( $P(\text{hur}) = 0.081$ ), the absolute difference in fitness is a bit lower, 0.0795, and the proportional reduction in fitness is a bit higher, 6.0%. This means that, given current natural conditions, plant fitness, as measured by the stochastic growth rate, is reduced by 6.0% by moths.

Hurricane frequency also has a much larger effect than moths on the mean fecundity of large reproductive plants over the entire temporal sequence of environments. The peak effect of moths on the mean fecundity also occurs when  $P(\text{hur}) = 0.1215$ . Increasing hurricane frequency increases the mean but decreases the variability of fecundity, while introducing moths not only decreases the mean, but also increases the variability of fecundity (see Appendix D). We do not dwell on details of effects of moths and hurricanes on mean fecundity itself, since this parameter is only a fitness component, not a measure of overall fitness. We are more interested in how sensitive the stochastic growth rate is to changes in fecundity in particular states of the habitat.

*Habitat-stage fecundity elasticity: no moths at the historical hurricane frequency*

The main issue here is to examine how sensitive fitness is to changes in life-history rates in particular environments. Recall that when summed over all life-history rates and all habitats, the habitat-stage elasticities will sum to 1. Thus we are searching for the elements that make the biggest contribution to total elasticity. We first focus on the scenario of no moths at the historical hurricane frequency.

The stochastic growth rate is not very sensitive to changes in fecundity in any state of the habitat. Fe-

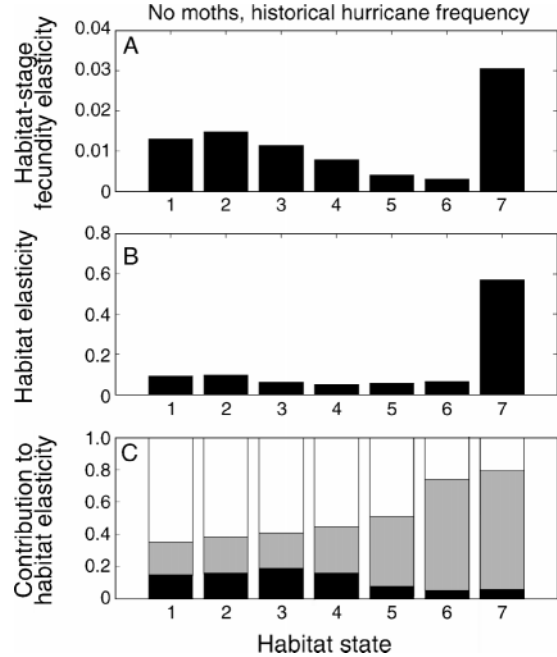


FIG. 3. Habitat-stage elasticity and its two components for fecundity (summed across all relevant stages) for the ideal world of no moths, at the historical hurricane frequency. (A)  $\sum e_{i,j,\beta}$  for  $i = 1$ , all  $j$ , for each  $\beta$  is the habitat-stage elasticity for fecundity; (B)  $\sum e_{i,j,\beta}$  for all  $i$  and  $j$ , for each  $\beta$  is the habitat elasticity; and (C)  $(\sum e_{i,j,\beta} \text{ for a given type of life-history rate}) / (\sum e_{i,j,\beta} \text{ for all } i \text{ and } j)$  is the proportion of habitat elasticity contributed by particular types of life-history rates (fecundity, black; stasis, gray; growth, white) within each habitat. The contribution of regression is too small to be visible.

cundity elasticity summed across all  $\beta$ 's only accounts for 8.5% of total elasticity. We investigate for which state of the habitat would small changes in fecundity have the greatest impact on the stochastic growth rate. Habitat-stage fecundity elasticities ( $\sum e_{i,j,\beta}$  for  $i = 1$ , all  $j$ , for each  $\beta$ ) address this issue (Fig. 3A). The darkest state of the habitat, 7, has higher habitat-stage fecundity elasticity than other states (Fig. 3A).

There are two factors that determine the magnitude of habitat-stage elasticity. The first is the frequency of the habitat state in the temporal sequence,  $\sum e_{i,j,\beta}$  for all  $i$  and  $j$ , for each  $\beta$ , gives the habitat elasticity or equivalently the frequency of the habitat state. Fig. 3B shows that state 7 is indeed more frequent in the sequence. The second factor (shown in Fig. 3C) compares the relative contribution of fecundity with that of regression, stasis, and growth to the habitat elasticity. It might have been that fecundity contributed a high proportion to the elasticity of state 7, however this was not the case (Fig. 3C). By way of contrast, examine state 2, second in importance in fecundity elasticity (Fig. 3A). There is a greater contribution of fecundity to habitat elasticity of state 2 than of state 7 (Fig. 3C), so that is a factor for state 2 rather than simply its frequency (Fig. 3B). In summary, at the historical hur-

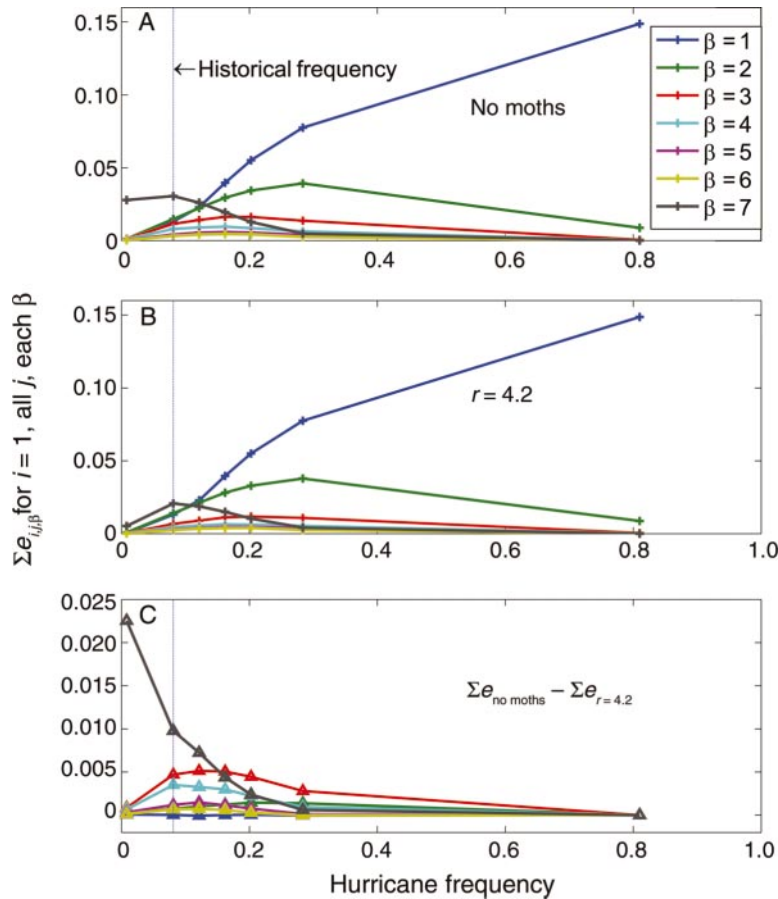


FIG. 4. Effects of hurricanes and moths on habitat-stage elasticity for fecundity. Two moth-dynamics scenarios are depicted: (A) an ideal world of no moths and (B) a world where moth abundance increases rapidly,  $r = 4.2$ . Differences between the two scenarios are shown in (C). Seven hurricane frequencies were investigated (Appendix C). The historical hurricane frequency is indicated by a vertical line.

ricane frequency, which represents current natural conditions, events in the darkest state of the habitat (state 7) dominate the stochastic dynamics of the plant, and the stochastic growth rate is quite insensitive to fecundity perturbations within this state.

Thus, this analysis shows us that it is not surprising that an animal like our moth, whose biggest stage-specific impact is on fecundity rates in habitat state 7, has relatively little impact on the stochastic growth rate. However, the habitat-stage elasticity analysis up to here concerns a small perturbation of fecundity. What further insights may be obtained by adding moths to the model (changing fecundity in the complex way that they actually do when they recolonize) and changing the disturbance regime? How does the elasticity behave and how does this help us to understand our results?

*Habitat-stage fecundity elasticity: adding moths and varying hurricane frequency*

*Habitat-stage elasticities.*—Fecundity elasticity in the lightest state of the habitat (state 1) increases with

hurricane frequency (Fig. 4A) as does its frequency in the environment (Fig. 2C), while that of state 2 peaks at  $P(\text{hur}) = 0.1620$ , as does its frequency in the environment. For these two light states, the hurricane effect is, perhaps surprisingly, independent of the presence of moths (Fig. 4C). When these states dominate, the magnitude of fecundity elasticity overall is higher, suggesting that we might expect a large effect of moths. However, in our system moths are not found in these states, even at high rates of moth recolonization (Appendix A) and there is no opportunity for them to affect the dynamics.

In contrast, moths can be abundant in the darkest state of the habitat (state 7) (Appendix A). Thus, this is the state of the habitat that exhibits the largest effect on elasticity of adding moths (Fig. 4C), but only at low hurricane frequencies, when it very strongly dominates the environment. Adding moths at low hurricane frequencies to already dark habitats with low seed production, lowers not only the fecundity itself, but also lowers the sensitivity of the stochastic growth rate to fecundity (Fig. 4C).

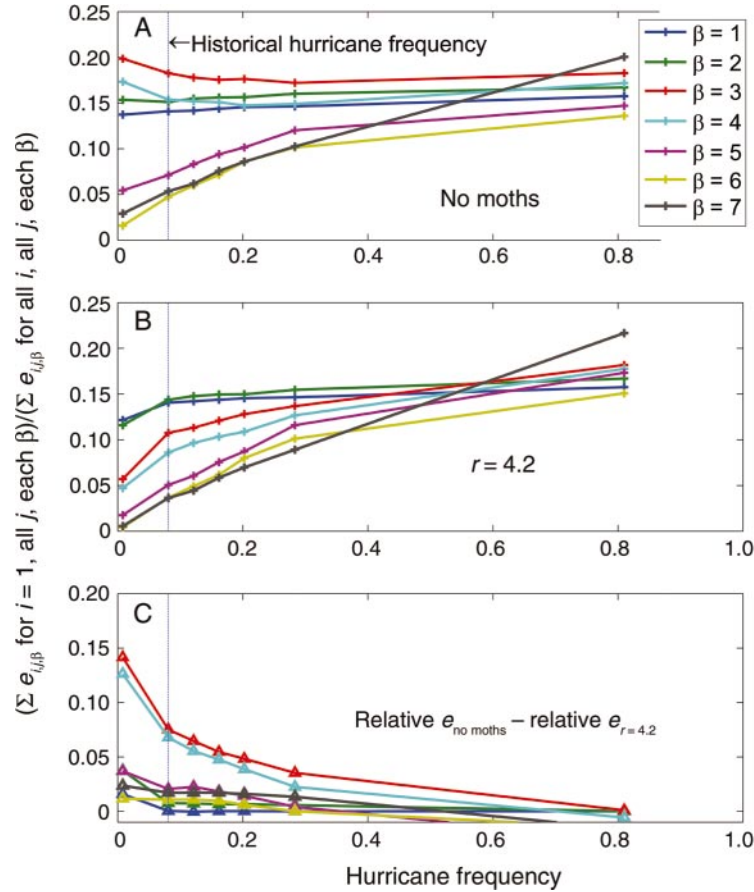


FIG. 5. Effects of hurricanes and moths on the contribution of fecundity to habitat elasticity. Two scenarios of predator abundance are depicted: (A) an ideal world of no moths and (B) a world where moth abundance increases rapidly,  $r = 4.2$ . Differences between the two scenarios are in (C). Seven hurricane frequencies were investigated (Appendix C). The historical hurricane frequency is indicated by a vertical line.

Habitat-stage fecundity elasticity of states 3 and 4 also are lowered by adding moths, but only at intermediate hurricane frequencies, with peak effects on elasticity, respectively, at  $P(hur) = .1215$  and  $P(hur) = 0.0810$ . This result is not explained by the frequencies of these states in the environment, but it is best understood by examining the contribution of fecundity to habitat elasticity of these two states.

*Habitat elasticities.*—The habitat elasticities are the same as the statistically stationary frequencies of habitat states (Fig. 2C) and are not affected by moths.

*Contributions of fecundity to habitat elasticity.*—The effects of moths and hurricanes on the contributions of fecundity to habitat elasticities are complicated and fascinating. Fig. 5 depicts the contribution of fecundity (vs. the other types of transitions, which are not pictured) to habitat elasticities for each state of the habitat. These elasticities contain information about expected changes in the future environment. The patterns fall into three groups: (1) the three darkest habitats, 5, 6, and 7; (2) the two lightest habitats, 1 and 2; and (3) two intermediate habitats, 3 and 4 (Fig. 5).

First, the contribution of fecundity to elasticity of dark states (5, 6, and 7) are low at low hurricane frequency but increase with hurricane frequency, in both the presence and absence of moths. (Fig. 5A and B). This is interesting because these dark habitats do not themselves increase in frequency as hurricanes increase in frequency—quite the contrary (Fig. 2C).

Second, the contribution of fecundity to elasticity of light states 1 and 2 is relatively stable at about 10–15% across hurricane frequencies, in both the presence and absence of moths, except at the very lowest hurricane frequency in the *rapid-recolonization* scenario (Fig. 5A and B).

Third, moths markedly alter the response of elasticity structure to hurricane frequency for intermediate states 3 and 4 (Fig. 5C). In the absence of moths, fecundity contributes 15–20% to the habitat elasticity of states 3 and 4 (Fig. 5A). In the presence of moths, the relative importance of fecundity for states 3 and 4 increases monotonically from near 5% to around 20% at the highest hurricane frequency (Fig. 5B). Putting these two patterns together, we see that moths decrease the con-

tribution of fecundity to habitat elasticity of states 3 and 4, especially at low hurricane frequency, where the effect is as much as a 10% difference (Fig. 5C).

*Relating components back to overall habitat-stage fecundity elasticity.*—The relative importance of states 3 and 4 is higher than would be predicted by their frequency, especially in the absence of moths. This elevation of importance is due to their prominent role in the contribution of fecundity to habitat elasticity (Fig. 5). The pattern can be most clearly seen by focusing on the difference between the moth scenarios (Figs. 4C and 5C).

#### DISCUSSION

Our study emphasizes several important aspects of plant–animal interactions in random environments. First, the appropriate parameter for studying the effects of animals on plant fitness in random environments is the stochastic growth rate (Tuljapurkar 1982). Thus, to analyze the effects of an animal on plant fitness, we need to know not only its effects on particular vital rates in each state of the environment and the relative frequency of those states, but also the expected temporal pattern of variation among the states and rates. The second point of general importance is that the consequences of these factors are revealed only by analysis of the stochastic dynamics, including the habitat-stage elasticity. This new parameter contains information about the expected future sequence of states of the habitat. The expected future alters the sensitivity of fitness to current events. The same event in the context of one future would have a different meaning in the context of a different future. Our understanding of the stochastic dynamics was enhanced by comparing the fitness effects of fecundity perturbations across disturbance frequencies and moth-recolonization dynamics. Disturbance regime altered the expected future sequence of states of the habitat and moth-recolonization dynamics altered the expected state-specific impact of moths on plants. The two factors interacted to provide new insights.

#### *Effects of moths on the stochastic growth rate, $\lambda_s$ , and on fecundity*

There are three general conclusions for this section. First, an animal's effect on a single vital rate in a frequent state of the habitat is *not* a measure of its impact on fitness. This result is not surprising to plant demographers who are used to the idea that a fitness component is not the same as fitness. However, what is a new emphasis in this paper is that the effect on the long-term dynamics is not the same as its effect on the demographic quality of the most frequent state of the environment (given by an eigenvalue analysis of the demography of that single state). In our study system a moth destroyed nearly 90% of the fruits in the most frequent state of the habitat, but reduced the stochastic growth rate by only about 6% (at the historical hurri-

cane frequency). If there were a plant phenotype characterized by a trait that was able to exclude all moths, the advantage to that phenotype would at maximum be 6%.

That an effect on a single vital rate is not the same as an effect on population growth rate is well known in the demographic literature for time-invariant models and is beginning to become known in the plant–animal interaction literature (Ehrlén 1995, 2003), especially with respect to biological control of invasive plants (Parker 1997, 2000, Shea and Kelly 1998, McEvoy and Coombs 1999). What is new here is the habitat-stage analysis for a varying environment. Our results show that a single-state demographic analysis of a plant–animal interaction in the most frequent state of the habitat will provide only limited insight into its effect on the long-run success of the plant population when there is temporal variation in demography. Bastrante et al. (1995) also found an interaction of environmental variability and herbivores in their effects on plant fitness. Most relevant was that the sequencing of environments mattered in their study. Long-run growth was actually favored by series that included several “poor” years being followed by a good year. In poor years the age structure shifted to favor large plants that can profusely produce seeds in good years; the population was dominated by these super producers in good years, overcompensating for the series of poor years. This example also shows that the evaluation of a habitat as “poor” from its single-habitat viewpoint may be incomplete. The value of a current demographic event for long-run growth will depend upon the future states of the habitat.

Second, the effects of an animal on the stochastic growth rate depends upon the disturbance regime. In exploring hurricane frequencies over two orders of magnitude, we found a maximum effect of animals on the stochastic growth rate at an intermediate frequency of disturbance. This particular result emerges from the biology of our system. Moths have a small effect in the highly disturbed environment, which is dominated by a state that has low probability of moth recolonization and high persistence, even though it has relatively high fecundity elasticity. Moths also have a small effect in the relatively undisturbed environment but for a different reason; this environment is dominated by a state that has high probability of moth occupancy, high persistence, but low fecundity elasticity. Here, adding moths does affect a vital rate in that state; but the stochastic growth rate is relatively insensitive to perturbations of this vital rate in that state. Intermediate rates of disturbance result in a more dynamic habitat, one in which an uncolonized state is more likely to become a colonized state and a state with low elasticity is more likely to become a state with high elasticity. The way these environmental transitions affect the stochastic growth rate is encapsulated by the habitat-stage elasticity.

Third, the exclusion of an animal could change not only the mean, but also the variance of a vital rate across time by amounts that depend upon the disturbance regime.

*Effects of moths and hurricanes on habitat-stage fecundity elasticity*

The stochastic growth rate is differentially sensitive to events (interactions with animals or any other event that affects a vital rate) in different states of the habitat as a result of two factors: the frequency of the state in the environment and the contribution of each life-history transition to habitat elasticity. The latter is the more interesting. Our habitat-stage elasticity is conditional upon being in state  $\beta$  at time  $t$ ; in a sense it “integrates” over expected future sequences of habitats. In contrast to elasticity in a time-invariant model, here the relative importance of life-history transitions in a given state is influenced by future states of the environment.

Recall the contribution of fecundity to habitat elasticity in the context of a changing disturbance regime. The value of making seeds in the three darkest states of the habitat increases with hurricane frequency because in that case today’s dark habitats are more likely to become lighter. Light environments are better for growth and reproduction. The value of making seeds in the two lightest states of the habitat is relatively independent of the rest of the environmental context, because at all but the lowest hurricane frequencies, the expected proximal sequence of states is likely to be beneficial for growth and survival. The value of making seeds in intermediate states of the habitat that are relatively low frequency, is complexly related to moths, hurricane frequency, and the expected pattern of future habitat states. The fitness benefit of making more seeds when a population is in state 3 is complex both because the disturbance regime can markedly alter the expected sequence of future states and because the predator alters the demographic quality of these states.

Finally, the presence of the plant–animal interaction itself may alter the sensitivity structure. When animals lower a life-history rate they may also lower the proportional sensitivity of population growth to that rate. In the absence of moths, the stochastic growth rate is more sensitive to fecundity changes in states 3 and 4 than when moths are present. Thus, animals not only lower the value of the vital rate in these habitats but also lower the sensitivity of the stochastic growth rate to the vital rate. More generally, the plant–animal interaction “pushes” the system towards an altered sensitivity structure, altering the selective regime. This is not simply an artifact of the additivity of elasticities but it is a biologically interesting result.

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#### APPENDIX A

The models of moth population dynamics are available in ESA's Electronic Data Archive: *Ecological Archives* E086-182-A1.

#### APPENDIX B

The relation between Tuljapurkar's and Caswell's equations describing population growth in stochastic environments is described in ESA's Electronic Data Archive: *Ecological Archives* E086-182-A2.

#### APPENDIX C

Information about hurricane frequencies chosen for further study is available in ESA's Electronic Data Archive: *Ecological Archives* E086-182-A3.

#### APPENDIX D

Effects of moths on the mean and variability of the fecundity of large reproductive plants are presented in ESA's Electronic Data Archive: *Ecological Archives* E086-182-A4.