Food limitation and insect outbreaks: complex dynamics in plant–herbivore models

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Summary

1. The population dynamics of many herbivorous insects are characterized by rapid outbreaks, during which the insects severely defoliate their host plants. These outbreaks are separated by periods of low insect density and little defoliation. In many cases, the underlying cause of these outbreaks is unknown.

2. Mechanistic models are an important tool for understanding population outbreaks, but existing consumer–resource models predict that severe defoliation should happen much more often than is seen in nature.

3. We develop new models to describe the population dynamics of plants and insect herbivores. Our models show that outbreaking insects may be resource-limited without inflicting unrealistic levels of defoliation.

4. We tested our models against two different types of field data. The models successfully predict many major features of natural outbreaks. Our results demonstrate that insect outbreaks can be explained by a combination of food limitation in the herbivore and defoliation and intraspecific competition in the host plant.

Key-words: consumer–resource model, difference equation model, herbivory, population dynamics, *Trirhabda*.

Introduction

Populations of many herbivorous insects undergo outbreaks, in which short-lived peaks of high density and massive defoliation alternate with long periods of low density (Varley, Gradwell & Hassell 1973; Crawley 1983; Berryman 1987; Myers 1988; Logan & Allen 1992). Because of the long time scales involved, identifying the causes of these fluctuations empirically is difficult (Liebhold & Kamata 2000), so mathematical models provide key tools for understanding insect outbreaks. Most models assume that outbreaks are driven by parasitoids and pathogens (e.g. Hairston, Smith & Slobodkin 1960; Hassell 1978; Anderson & May 1980; Murdoch, Briggs & Nisbet 2003; Turchin *et al.* 2003), on the grounds that parasitoid and pathogen attack rates are often high during outbreaks (Hassell 1978; Anderson & May 1980). Host–pathogen and host–parasitoid models can indeed produce long-period, large-amplitude cycles that resemble time series of insect outbreaks (Kendall *et al.* 1999; Turchin *et al.* 2003);

nevertheless, for some insect herbivores, intraspecific competition is clearly more important than natural enemies for population regulation (Carson & Root 1999, 2000; McEvoy 2002; Bonsall, van der Meijden & Crawley 2003; Long, Mohler & Carson 2003). In an effort to understand outbreaks in such species, here we construct and analyse plant–herbivore models in which food limitation drives insect population dynamics.

Models applied to plant–herbivore interactions are usually modified versions of Lotka–Volterra predator–prey models (Caughley & Lawton 1981; Crawley 1983; Grover & Holt 1998; Das & Sarkar 2001, but cf. Buckley *et al.* 2005). Like most consumer–resource models, these models show 'prey–escape' cycles in which the plant acts as prey, rising briefly to high densities before being decimated by rising herbivore densities. In nature, by contrast, the densities of plants that are attacked by outbreaking herbivores are usually high for long periods, with only brief periods of high defoliation (McNamee, McLeod & Holling 1981; Crawley 1983; Berryman 1987). Indeed, the observation that defoliation is low much of the time inspired the general argument that plants and their herbivores do not regulate each other (Hairston *et al.* 1960; Lawton & McNeill 1979; Price *et al.* 1980). Nevertheless, others have argued that

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herbivores may be food-limited, and plant densities may be affected by herbivores, even if obvious defoliation is infrequent (Murdoch 1966; Ehrlich & Birch 1967). Here we attempt to provide a quantitative framework for the latter argument.

By constructing models that realistically describe the biology of herbivorous insects and their host plants, we show that it is possible to explain insect outbreaks through a combination of food limitation in the herbivore and defoliation and intraspecific competition in the host plant. Unlike the prey-escape cycles predicted by classical models, outbreaks in our models are characterized by high plant abundance during the inter-outbreak period, more closely matching patterns of defoliation observed in natural systems. Our results show that herbivore food limitation does not necessarily suggest prolonged periods of severe defoliation, and that realistic insect outbreaks can result from plant–herbivore interactions alone.

Methods

As we have described, models that are applied to plant–herbivore interactions are often consumer–resource models that show prey-escape cycles (Pacala & Crawley 1992; Nisbet *et al*. 1997; Huisman & Olff 1998; Trumper & Holt 1998). Figure 1(a) shows that, for the well known Rosenzweig–MacArthur model, low consumer densities allow the resource to escape strong consumption temporarily and increase quickly, but over-exploitation eventually causes both populations to crash. Although the prey may approach its peak density more gradually than the consumer (Turchin 2003), prey-escape cycles ultimately predict that insect outbreaks should be preceded directly by relatively rapid and short-lived outbreaks in plant abundance. In nature, however, densities of the host plants of outbreaking insects are usually high for long periods, during which insect densities are correspondingly low. Periods of high plant abundance in such systems are punctuated by sudden insect outbreaks, followed by a rapid crash and rapid recovery of the host plant (McNamee *et al*. 1981; Crawley 1983; Berryman 1987). Prey-escape cycles thus do not capture a basic feature in outbreaking insect–plant systems. To document this lack of fit to data, we quantified the percentage of time that host plants are defoliated in several natural systems. To make comparisons between models and data, and between data sets that report different measures of defoliation, we defined periods of defoliation to be times during which plant abundance was <75% of the maximum abundance ever observed, although changing this cutoff somewhat did not alter our conclusions. The data in Table 1 show that defoliation by several outbreaking insects does indeed contradict the predictions of prey-escape cycles. We therefore set out to construct more realistic models of insect–plant interactions.

It is perhaps not surprising that consumer–resource models such as the Rosenzweig–MacArthur model do
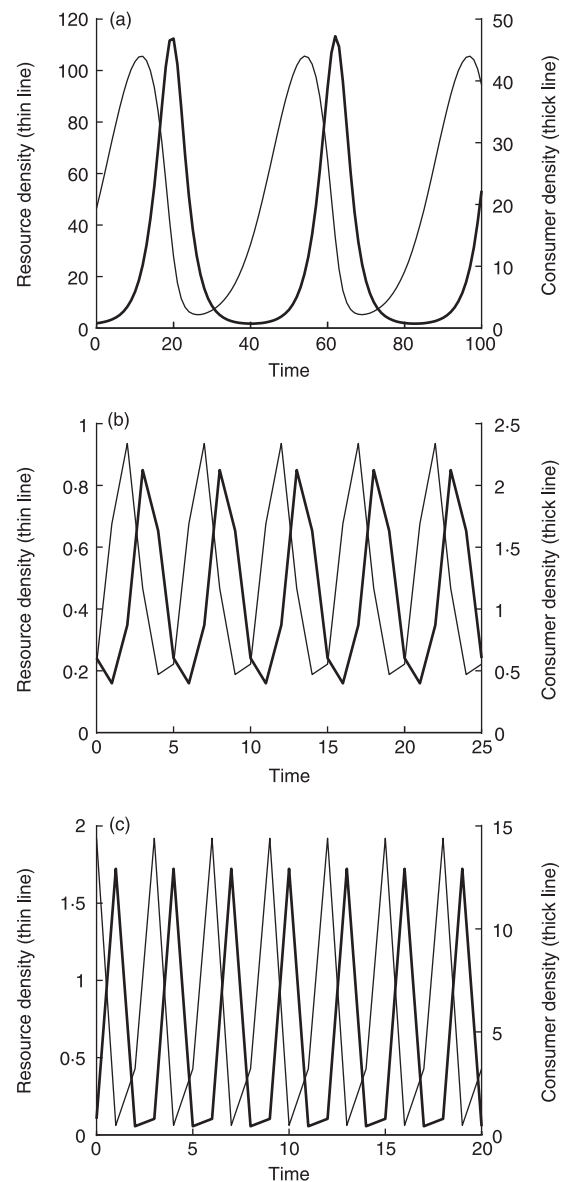
Fig. 1. Time series predicted by the Rosenzweig–MacArthur model and by density-dependent Nicholson–Bailey models. Thin lines correspond to the left-hand *y*-axes and represent resource abundances; thick lines on the right-hand axes are consumer abundances. Simulations were run for 10 000 generations with the last 20–100 generations shown. The models, in which N represents host density and P represents consumer density, are: (a) Rosenzweig–MacArthur model: $dN/dt = rN[1 - (N/K)] - aNP/(1 + aT_hN)$, $dP/dt = eaNP/(1 + aT_hN) - dP$ with $r = 0.2$, $K = 150$, $a = 0.02$, $T_h = 1$, $e = 1$, $d = 0.4$; (b) Nicholson–Bailey/type II model: $N_{t+1} = N_t\exp\{\rho(1 - N_t) - [P_t/(1 + \alpha N_t)]\}$, $P_{t+1} = \varphi N_t\{1 - \exp[-P_t/(1 + \alpha N_t)]\}$ with $\rho = 2.2$, $\alpha = 0.04$, $\varphi = 4$; (c) Nicholson–Bailey/type III model: $N_{t+1} = N_t\exp\{\rho(1 - N_t) - [N_t P_t/(1 + \alpha N_t + \gamma N_t^2)]\}$, $P_{t+1} = \varphi N_t\{1 - \exp[-N_t P_t/(1 + \alpha N_t + \gamma N_t^2)]\}$ with $\rho = 2.9$, $\alpha = 0.25$, $\gamma = 0.125$, $\varphi = 12.5$.

not match the population dynamics of outbreaking insects because such models are formulated in continuous time, whereas most outbreaking insects have discrete generations (Hunter 1991). However, well known discrete time consumer–resource models (after Nicholson

Table 1. Comparison of the percentage of time plants are defoliated in the model predictions and data

Insect species/ model name	Percentage of time plant experiences defoliation		Reference/equation
	Mean	Range	
Insect data			
Herbivores of *Solidago altissima*†	20·8	16·7–50·0	Root & Cappuccino (1992)
Orgyia pseudotsugata (Douglas fir tussock moth)	13·4	1·8–51·4	Shepherd *et al.* (1988)
Lymantria dispar (gypsy moth)	44·2	18·1–69·4	Leibhold, Elkinton & Muzika (2000)
Quadricalcarifera punctatella (beech caterpillar)	10·7	7·1–21·4	Leibhold, Kamata & Jacobs (1996)
Classical models			
Rosenzweig–MacArthur‡		69·1–92·1	Fig. 1a legend
Nicholson–Bailey/type II		48·5–96·0	Fig. 1b legend
Nicholson–Bailey/type III		45·1–98·0	Fig. 1c legend
Our models			
Ricker/type II		15·8–96·0	Equation 7
Ricker/type III		9·9–94·1	Equation 8
Beverton–Holt/type II		24·8–84·2	Equation 9
Beverton–Holt/type III		21·8–63·4	Equation 10

Minimum and maximum over a wide range of parameter values (see Appendix S1) are shown for the models. The average and range of reported time series are listed for data. We say a plant population is 'defoliated' if its abundance is <75% of the maximum observed abundance.

†Based on a total of five leaf-chewing insect species, including *Trirhabda virgata*, that consume *S. altissima*.

‡It is interesting to note that for parameter combinations that result in extremely infrequent outbreaks (e.g. 200 years between successive outbreaks), the Rosenzweig–MacArthur model can actually show defoliation as little as ≈25% of the time. However, when we exclude parameter combinations that result in fewer than one outbreak every 50 years (a very loose constraint, given that outbreaking insects typically peak every 8–12 years; Liebhold & Kamata 2000), we find the range of defoliation times reported here.

1933; Nicholson & Bailey 1935) also show prey-escape cycles (Fig. 1b,c), so this disparity is not limited to continuous-time models. In contrast to the assumptions of the Nicholson–Bailey model, insect and plant survival rates often appear to be non-linear functions of plant and insect density, respectively (Harper 1977; Crawley 1983). In our discrete-time models, we therefore assume that herbivore population growth is a non-linear function of herbivore feeding rate, and that plant population growth decreases gradually with increasing herbivory. Also, and again unlike the Nicholson–Bailey models, we assume that the herbivore feeding rate depends on plant density, rather than on herbivore density (Crawley 1983). A final key feature of many plant–herbivore interactions is that, in the absence of the herbivore, plant population density is regulated by intraspecific competition (Harper 1977; Antonovics & Levin 1980; Watkinson 1980), so we allow for density dependence in the plant.

Given these general considerations, we constructed our models as follows. X_t represents the density of edible plant biomass in generation t and Y_t represents the population density of the herbivore. Plant population growth is described by the function $f(X_t)$, while the effect of the herbivore on the plant's population growth rate is described by the function $g(Y_t)$. We assume that herbivore population growth is proportional to a non-linear, saturating function of plant density, $h(X_t)$. The structure of our models is:

$$X_{t+1} = rX_t f(X_t) g(Y_t), \tag{eqn 1a}$$

$$Y_{t+1} = sY_t h(X_t), \tag{eqn 1b}$$

where r and s are the maximum population growth rates for plant and herbivore.

To ensure our results are robust to changes in model structure, we consider two different functions for plant self-limitation. The first is the Ricker model:

$$f(X_t) = \exp(-mX_t), \tag{eqn 2}$$

where larger values of m represent stronger density dependence in the plant's growth rate. The second form of plant self-limitation is the Beverton–Holt model:

$$f(X_t) = 1/(1 + nX_t), \tag{eqn 3}$$

in which larger n represents stronger plant self-limitation.

Many consumer–resource models assume a non-linear relationship between resource population size and attack rate (Beddington 1975; Tang & Chen 2002). For plants and insect herbivores, we similarly expect a non-linear functional relationship, due to herbivore foraging time and satiation, but the relationship is expressed in terms of plant biomass units rather than population size, because herbivory is unlikely to kill entire plants (Harper 1977; Crawley 1983). Although

little is known about consumption rates at low plant density, there is abundant evidence that herbivory plateaus when food is at high density (Solomon 1981; Crawley 1983; Morris 1997; Rhainds & English-Loeb 2003). Two useful ways to represent such consumption rates are type II and type III functional responses. To ensure our results are robust to changes in functional form, we consider both. For type II, we have:

$$g(Y_t) = a/(b + Y_t), \tag{eqn 4a}$$

$$h(X_t) = pX_t/(q + X_t), \tag{eqn 4b}$$

For type III we have:

$$g(Y_t) = c/(d^2 + Y_t^2), \tag{eqn 5a}$$

$$h(X_t) = uX_t^2/(v^2 + X_t^2). \tag{eqn 5b}$$

In the absence of herbivores, the plant attains a fraction a/b (type II) or c/d^2 (type III) of the population growth rate given by $f(X_t)$. b and d are the densities of herbivores required to reduce these fractions to half their maxima. With abundant food, herbivore survivorship will equal p (type II) or u (type III). q and v give the density of edible plant biomass that causes a 50% reduction in herbivore survival.

We begin our analyses by non-dimensionalizing the four resulting models (each form of plant density dependence with each set of interaction terms). Non-dimensionalization is an algebraic manipulation that allows state variables to be measured in scale-independent units, reducing the number of parameters and simplifying the analysis of the models. When non-dimensionalized, each model has only three parameters. For instance, the discrete-time analogue of the Rosenzweig–MacArthur model has Ricker density dependence in the plant (equation 2) and type II interaction terms (equation 4):

$$X_{t+1} = rX_t \exp(-mX_t)a/(b + Y_t), \tag{eqn 6a}$$

$$Y_{t+1} = sY_t \, pX_t/(q + X_t). \tag{eqn 6b}$$

Substituting $R_t \equiv mX_t$, $N_t \equiv Y_t/b$, $\lambda \equiv ar/b$, $\omega \equiv sp$ and $\beta \equiv qm$ into equation 6 gives:

$$R_{t+1} = \lambda R_t \exp(-R_t)/(1 + N_t), \tag{eqn 7a}$$

$$N_{t+1} = \omega N_t \, R_t/(\beta + R_t), \tag{eqn 7b}$$

where R_t represents the density of edible plant biomass and N_t represents herbivore density, with each in dimensionless units. Similarly, the Ricker/type III model becomes:

$$R_{t+1} = \lambda R_t \exp(-R_t)/(1 + N_t^2), \tag{eqn 8a}$$

$$N_{t+1} = \omega N_t R_t^2/(\beta + R_t^2), \tag{eqn 8b}$$

when non-dimensionalized. The Beverton–Holt/type II model becomes:

$$R_{t+1} = \lambda R_t/[(1 + R_t)(1 + N_t)], \tag{eqn 9a}$$

$$N_{t+1} = \omega N_t \, R_t/(\beta + R_t), \tag{eqn 9b}$$

and the non-dimensionalized Beverton–Holt/type III model is:

$$R_{t+1} = \lambda R_t/[(1 - R_t)(1 + N_t^2)], \tag{eqn 10a}$$

$$N_{t+1} = \omega N_t R_t^2/(\beta + R_t^2). \tag{eqn 10b}$$

In all four models, ω, λ and β describe the maximum insect and plant population growth rates and the strength of food limitation, respectively. Larger values of β mean that the herbivore is more severely food-limited.

Natural populations experience fluctuations in environmental conditions from year to year, and insects are known to be particularly susceptible to the density-independent effects of weather (Williams & Liebhold 1995; Andresen *et al*. 2001; Redfern & Hunter 2005), so it is important to consider stochasticity in insect dynamics. We achieved this by replacing ω in equations 7–10 with $\exp(\varepsilon_t)\omega$. Values of ε_t were normally distributed with mean zero and variance σ^2 and were independently drawn in each time step.

For cases in which the models exhibited chaos, we calculated Lyapunov exponents, using the methods described by Dennis *et al*. (2001). Chaos is indicated by positive global Lyapunov exponents (GLEs) and is characterized by an erratic predicted time series. Local Lyapunov exponents (LLEs) give the rate of trajectory divergence from a particular set of initial conditions over a short time interval. For a chaotic cyclic attractor, the magnitudes of LLEs calculated at points around the cycle identify the points that contribute most to the chaotic GLE. Positive (chaotic) LLEs also tell us where in phase space stochasticity will most strongly amplify deterministic chaos.

We tested our models in several ways. First, both for our models and for some common consumer–resource models, we ran simulations to examine whether the models can produce dynamics that qualitatively resemble the pattern of short periods of defoliation followed by long periods of high plant biomass. We compared the minimum and maximum defoliation levels predicted by each model against defoliation data for several species (Table 1). We constructed Table 1 by simulating each model over a very broad range of parameter values (Appendix S1 in Supplementary material) and calculating the proportion of the time the plant was below 75% of its maximum abundance for each parameter combination. We excluded simulations that did not exhibit reasonable outbreak behaviour (those that were not outbreaking at all and those outbreaking less frequently than once every 50 years), then reported the range of defoliation intensities displayed by the remaining simulations in the table.

Second, we used experimental and observational data on *Solidago altissima* L. and its outbreaking specialist herbivores, *Trirhabda virgata* LeConte, *Trirhabda borealis* Blake and *Trirhabda canadensis* Kirby, to estimate parameter values for our models. We used Akaike's information criterion (AIC) to gauge the support the data provide for the functions we used in constructing our models relative to linear alternatives. AIC takes into account both the better fit and the reduced parsimony provided by models with more parameters, such that the model with the smallest AIC value provides the best explanation for the data. Models with AIC differences (AIC values minus the smallest observed AIC value) smaller than ≈2 are supported by the data almost as well as the best model, whereas models with AIC differences of ≈4 or greater have much weaker empirical support than the best model (Burnham & Anderson 2002). Using the fitted parameter estimates, we compared the models' predictions to observational data on this system. We chose *Solidago* and *Trirhabda* for this example because there are abundant data on the details of their interaction, and because they fit the major assumptions of our models. In particular, there is evidence that *Solidago* is self-limited (Hartnett & Bazzaz 1985), that leaf-chewing by *Trirhabda* can reduce *Solidago* population growth (Sholes 1981; McBrien, Harmsen & Crowder 1983; Cain, Carson & Root 1991;

Meyer & Root 1993; Long *et al.* 2003), and that *Trirhabda* are food-limited (Brown & Weis 1995; Blatt, Schindel & Harmsen 1999; Appendix S2). *Trirhabda* are univoltine and the perennial *Solidago* grows new above-ground shoots each year, so both the edible plant biomass and the insect population are well described by discrete-time models. Above all, empirical data suggest that interactions with the host plant are important for driving *Trirhabda* population dynamics (Brown & Weis 1995; Herzig 1995), and that positive density dependence in parasitism rates, which is believed to drive the outbreaks of many insects (Hassell 1978; Anderson & May 1980), does not occur in this system (Messina 1983). The three common *Trirhabda* species are ecologically very similar (Messina & Root 1980; Messina 1982; Meyer & Whitlow 1992; Hufbauer & Root 2002), so in estimating parameters we assumed that the differences among them occur at a level of detail not considered by our models. Parameter estimates were obtained by maximum likelihood, with bootstrapped 95% confidence intervals, assuming normally distributed error.

Results

Each of the models (equations 7–10) shows realistic outbreaks with high plant biomass in the inter-outbreak period (Fig. 2). In general, the proportion of the time
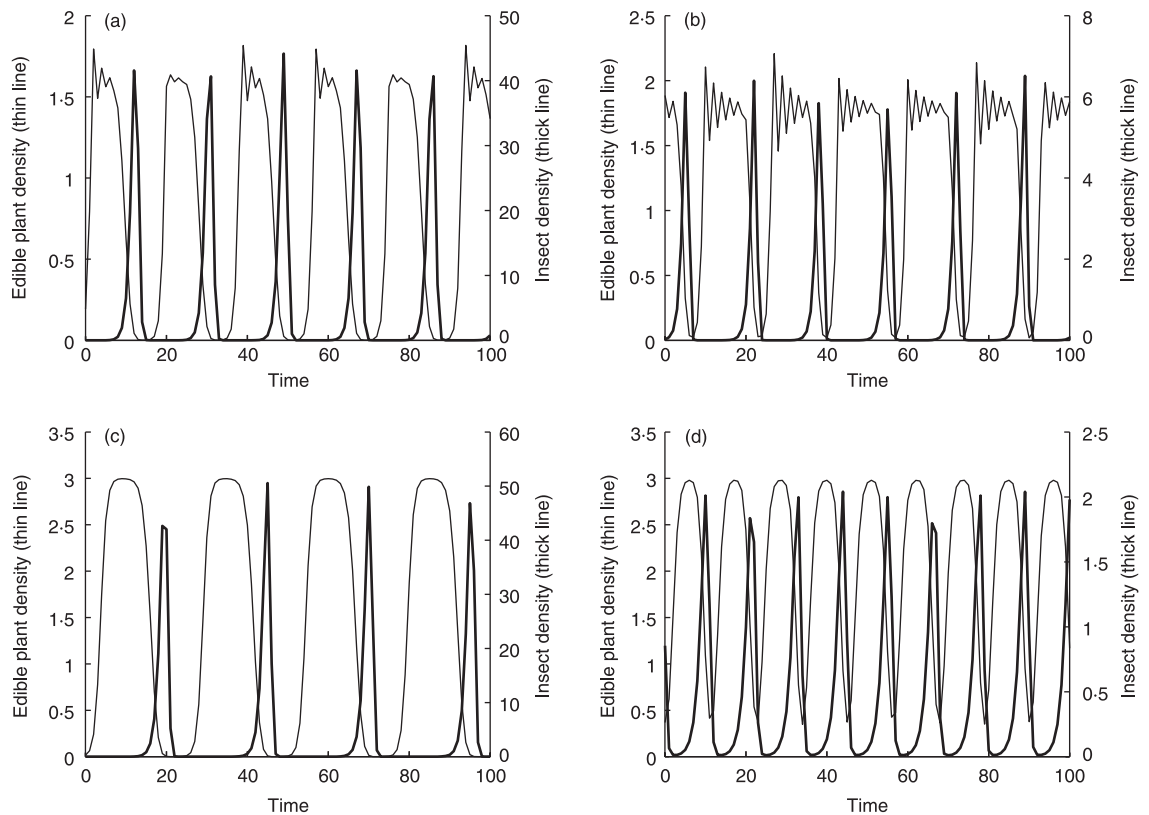
Fig. 2. Time series predicted by our models (equations 7–10). Thin lines correspond to left-hand *y*-axes and represent plant densities; thick lines on the right-hand axes are herbivore densities. Simulations were run for 10 000 generations with the last 100 generations shown. Models shown are: (a) Ricker/type II with σ = 0, λ = 5, ω = 4, β = 0·2; (b) Ricker/type III with σ = 0, λ = 6, ω = 4, β = 0·8; (c) Beverton–Holt/type II with σ = 0, λ = 4, ω = 3, β = 0·07; (d) Beverton–Holt/type III with σ = 0, λ = 6, ω = 4, β = 7.
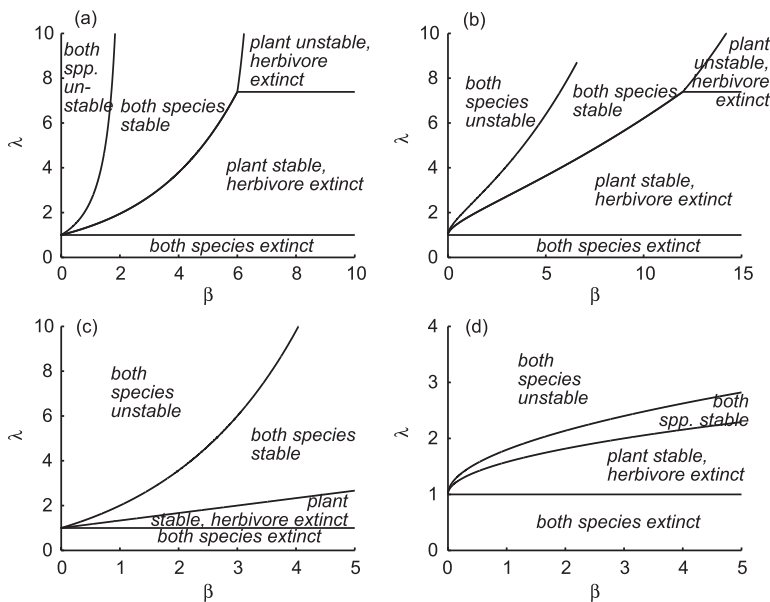
Fig. 3. Behaviour of our models (equations 7–10) with $\sigma = 0$ and $\omega = 4$: (a) Ricker/type II; (b) Ricker/type III; (c) Beverton–Holt/type II; (d) Beverton–Holt/type III. Larger values of λ represent higher plant population growth rates; larger values of β represent stronger food limitation in the herbivore. Cycles, outbreaks and deterministic chaos occur within the region labelled 'both species unstable'.

the plant experiences defoliation decreases as ω increases and as λ and β decrease. These cycles are qualitatively different from the prey-escape cycles predicted by other consumer–resource models (Fig. 1) in that the plant population spends a significant amount of time near its carrying capacity, matching field observations showing that defoliation occurs only rarely (Table 1). Table 1 shows that traditional consumer–resource models are unable to reproduce this pattern. Specifically, traditional models predict that defoliation should occur about half of the time or more, whereas natural defoliation rarely occurs more than 50% of the time. Our plant–herbivore models, in contrast, can reproduce most of the range of observed defoliation frequencies and always have minima less than 25%. Our models can thus explain data on several different taxa, whereas traditional consumer–resource models cannot. For species such as *Orgyia pseudotsugata* and *Lymantria dispar*, there is overwhelming evidence for an important role of natural enemies (Dwyer, Dushoff & Yee 2004), and for such species our models thus serve as a useful starting point for more realistic models that incorporate both food limitation and natural enemy attacks. For *Trirhabda* and perhaps other old-field insects, however, we suspect that our models are realistic enough to be directly useful in their current formulation.

To understand what makes the outbreaks in our models so different from the outbreaks in classical consumer–resource models, we analysed our models by calculating their equilibria, and by carrying out linear stability analyses. Like many classical consumer–resource models, our models have two non-trivial equilibria. At one equilibrium, the plant and the herbivore coexist at a stable fixed point. At the other equilibrium,

the herbivore is extinct and the plant grows to its carrying capacity. In Fig. 3, we show how the qualitative behaviour of the models changes as plant population growth rate, λ, and the strength of food limitation, β, vary. Each equilibrium is stable in a distinct region of parameter space. Changing herbivore population growth, ω, changes the exact placement of the stability boundaries in β–λ space, but does not change the orientation of these boundaries relative to one another. For parameter combinations for which none of the equilibria are stable (regions labelled 'both species unstable' in Fig. 3), several different dynamic behaviours may occur. Just outside the region of stability, limit cycles arise. Further from the stability boundary, the limit cycle widens and the trajectory approaches the other two unstable equilibria, first the one at which both species are extinct, and second the one at which the insect is extinct but the plant is near its carrying capacity. This cycle yields the realistic outbreak behaviour shown in Fig. 2, in which the system remains near the boundary equilibrium during the inter-outbreak period. Near this equilibrium, food is abundant, so the small herbivore population temporarily escapes food limitation while again increasing to outbreak densities. Because classical discrete-time consumer–resource models assume a linear relationship between resources consumed and new consumers produced, cycles in such models never take trajectories that allow one species to remain at very high densities while the other is at very low densities. Constructing our models to describe insect–plant interactions accurately thus allows the unstable boundary equilibria to drive realistic outbreak behaviour.

Our analyses show that all four models exhibit the same range of dynamics. The only notable difference among the models is that Beverton–Holt density dependence causes the plant population to remain constant during the inter-outbreak period, whereas Ricker density dependence causes damped 2^n-point cycles (Fig. 2a,b). This is because when the insect population is at low density, the plant population behaves almost as it would in a single species model. Unlike the equilibrium of the single species Ricker model, the equilibrium of the single-species Beverton–Holt model is always stable. The same suite of dynamics is also produced by models with mixed interaction terms (based on a full analysis of the model using equations 2, 4a, 5b and simulations of the remaining three combinations of functional forms). It thus appears that the model in equation 1 is structurally stable, meaning that our results are robust to changes in the functional forms that we use.

For most species, the exact timing and size of outbreaks is unpredictable, even when the long-term tendency is for outbreaks to occur at fairly regular intervals. Reassuringly, all four models can show weak deterministic chaos that allows for this behaviour, by making outbreaks more variable without changing the long-term tendency toward cycles. Adding log-normally distributed noise
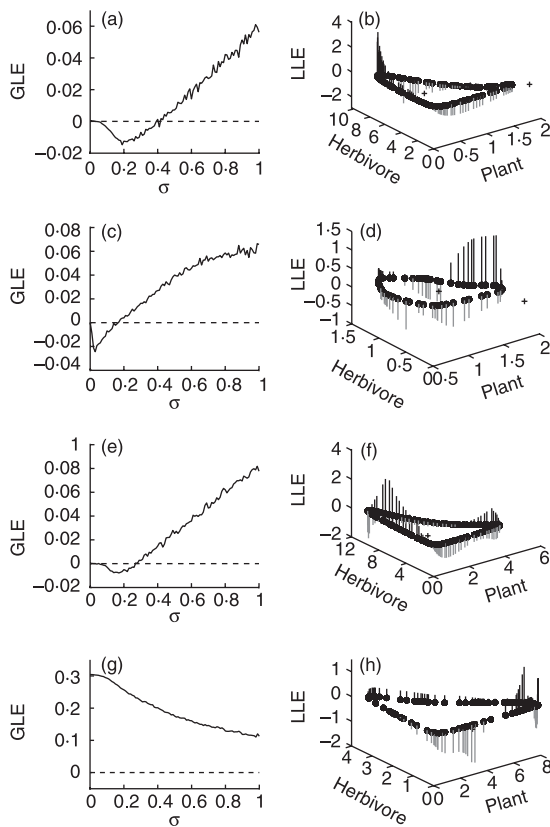
Fig. 4. Lyapunov exponents for: (a,b) Ricker/type II model with ω = 4, λ = 6, β = 1; (c,d) Ricker/type III model with ω = 4, λ = 6, β = 3·6; (e,f) Beverton–Holt/type II model with ω = 4, λ = 7, β = 2; (g,h) Beverton–Holt/type III model with ω = 2, λ = 9, β = 2·5. (a,c,e,g) Global Lyapunov exponents (GLEs) with varying degrees of stochasticity. Values above dashed line (positive GLEs) are chaotic. (b,d,f,h) Local Lyapunov exponents (LLEs) (σ = 0). The *x–y* plane represents phase space, with the two + signs showing population densities at the unstable coexistence and boundary equilibria. Black dots in this *z* = 0 plane show the limit cycle; vertical lines show the magnitudes of the LLE calculated at each point around the cycle for 10 time steps. Black lines indicate positive (chaotic) LLEs; grey lines indicate negative LLEs.

about the insect growth-rate term, ω, increases the strength of chaos in this range for three of the four models (Fig. 4a,c,e). Ordinary limit cycles do not exhibit chaos (Rand & Wilson 1991), so the deterministic chaos in these models is probably caused by the simultaneous influence of multiple unstable equilibria on the populations' trajectories. Similar results were found in the host–enemy models of Umbanhowar & Hastings (2002); Dwyer *et al*. (2004); Hall, Duffy & Cáceres (2005). The local Lyapunov exponents in our models tend to be highest when the insect population is building up (Fig. 4d,f,h) or crashing down (Fig. 4b,f), demonstrating that these transitions at the beginning and end of outbreaks are most responsible for the chaotic dynamics. Previous work has shown that periodic forcing can cause a system to switch chaotically between attractors (Henson *et al*. 1999; Dennis *et al*. 2001; Keeling, Rohani & Grenfell 2001), but further research is needed to understand how multiple unstable equilibria may interact to cause chaos.

Appendix S3 shows our parameter estimates for the *Solidago–Trirhabda* system and the type of data used for each estimate. In estimating model parameters, our intent was not to test the models' assumptions *per se*, but rather to demonstrate that the parameter estimates can be easily obtained from existing data. Nonetheless, we used AIC differences to gauge the support that the data provide for the functions in our models relative to simpler, linear alternatives. The linear models never provide the best fit to the data, and for plant density dependence and insect food limitation, our non-linear functions provide a substantially better explanation for the data than do the linear models (Table 2). The non-linear functions are shown with the data to which they were fitted in Appendix S3 (Figs S3.1–S3.3). For each of our non-linear models, we randomly drew 500 parameter combinations from the bootstrapped distributions for the *Solidago–Trirhabda* system. We then used these to calculate the non-dimensional parameters λ, ω and β for each of the random combinations. The resulting values of λ, ω and β lay within the outbreak region of parameter space in all 500 cases (Appendix S3, Figs S3.4, S3.5). As *Trirhabda* spp. do indeed outbreak (Messina & Root 1980; McBrien *et al*. 1983; Root & Cappuccino 1992; Brown & Weis 1995), our models accurately predict the qualitative dynamics of this system.

In carrying out a more quantitative comparison of models to data, we were limited by the lack of long-term time series of *Trirhabda* densities against which to compare the models' predicted time series. Furthermore, like any models with complex dynamics, our models are at least moderately dependent on initial population densities, and these are of course unknown. We therefore follow Kendall *et al*. (1999) in comparing summary statistics describing our model predictions with statistics reported for the *Solidago–Trirhabda* system. To avoid circularity, we used summary statistics from studies other than those from which we estimated parameter values. First, high *Trirhabda* densities last only a growing season or two (McBrien *et al*. 1983), which compares well with our model prediction that outbreaks should last an average of 1·9–2·3 years. Second, the maximum observed *T. virgata* densities over a 6-year period were approximately five times greater than the mean density (Root & Cappuccino 1992), which similarly compares well with our model predictions that the maximum density in six generations should be, on average, 5·7 (Ricker/type II), 5·8 (Ricker/type III and Beverton–Holt/type III) or 5·9 (Ricker/type III) times the mean. Finally, the standard deviation of log *T. virgata* abundances ranged from very small values to ≈1, with a median near 0·5 (Root & Cappuccino 1992), which is included in the range of our model predictions for standard deviations (1·2 for Ricker/type II, 0·5 for Ricker/type III, 1·4 for Beverton–Holt/type II and 0·4 for Beverton–Holt/type III). Our models thus successfully reproduce quantitative features of *Trirhabda* outbreaks in nature. Moreover, the data used to parameterize the models were collected over short spatial and/or temporal

Table 2. Likelihoods and Akaike's information criterion differences (ΔAIC) for the functions fitted to *Solidago–Trirhabda* data

Function	Equation	Number of parameters	Negative log-likelihood	ΔAIC
Plant density dependence				
Linear	$f(X_t) = c_1 - c_2 X_t$	2	9·9	12·3
Ricker	$r \times$ equation 2	2	5·9	4·3
Beverton–Holt	$r \times$ equation 3	2	3·7	0
Effect of insect on plant†				
Linear	$g(Y_t) = c_1 - c_2 Y_t$	2	−5·6	0·1
Type II	Equation 4a	2	−5·7	0
Type III	Equation 5a	2	−5·3	0·7
Effect of plant on insect				
Linear through origin	$h(X_t) = c_1 X_t$	1	44·0	12·0
Linear	$h(X_t) = c_1 + c_2 X_t$	2	38·7	3·4
Type II	Equation 4b	2	37·3	0·6
Type III	Equation 5b	2	37·0	0

Models with AIC differences = 0 are the best-fitting models. For models not described in the text, c_1 and c_2 represent fitted parameters. For models with negative slopes (plant density dependence and effect of insect on plant), we do not attempt to force the linear functions through the origin because this would prohibit positive values for the functions. The fitted non-linear functions are shown plotted with the data in Appendix S3.
†These AIC differences were calculated using AIC_C values, which are corrected for small sample size.

scales (Appendix S3), whereas the summary statistics used to test the models came from larger-scale studies: data in McBrien *et al.* (1983) were collected in six 100·5-m^2 plots over 5 years; data in Root & Cappuccino (1992) were collected in 22 fields exceeding 7 km^2 over 6 years. The tests of our models thus involved both independent parameter estimates and extrapolation across scales, two key ingredients in rigorous model testing (Tilman & Kareiva 1997).

Discussion

There are four well known hypotheses for the causes of outbreaks in herbivorous insects. The first is that outbreaks are driven by interactions with natural enemies, either through simple prey escape (Southwood & Comins 1976; Lawton & McNeill 1979; McCann *et al.* 2000; Maron, Harrison & Greaves 2001) or as a result of complex interactions with multiple enemies (Dwyer *et al.* 2004). The second is that outbreaks are caused by properties of plant tissues, such as inducible defences (Edelstein-Keshet & Rausher 1989; Busenberg & Velasco-Hernandez 1994; Lundberg, Jaremo & Nilsson 1994; Underwood 1999) or physiological stress (White 1984). The third is that outbreaks may result if an insect's performance is influenced by the conditions that its parents and grandparents experienced in preceding generations (Ginzburg & Taneyhill 1994). The fourth is that outbreaks are due to environmental forcing (Elton 1924; Andrewartha & Birch 1954; Hunter & Price 1998). Although none of these hypotheses explains all outbreaks, each is undoubtedly correct for some insects. In presenting a fifth hypothesis, our goal is thus

to provide an explanation for outbreaks in cases for which food limitation is the most important force driving insect dynamics. The literature on insect herbivory suggests that such cases may be common (Monro 1967; Carson & Root 1999, 2000; McEvoy 2002; Bonsall *et al.* 2003; Long *et al.* 2003; Rhainds & English-Loeb 2003).

Under the hypothesis embodied by our models, the plant–herbivore system oscillates between unstable equilibria. Between outbreaks, the plant approaches its herbivore-free equilibrium and the insect is at a very low density. Outbreaks occur when the insect population rises toward the limit cycle that surrounds the unstable coexistence equilibrium. These cycles match qualitative descriptions of plant–herbivore fluctuations more closely than do classical prey-escape cycles by showing high plant biomass during the inter-outbreak period (Table 1). Our models thus support the argument that vegetation can be abundant even if plants regulate herbivores through food limitation (Murdoch 1966; Ehrlich & Birch 1967).

Our models also survived more rigorous testing with data for the *Solidago–Trirhabda* system. When we estimated the model parameters from data for this interaction (Appendix S3), all four models correctly predicted that outbreaks should occur, and accurately reproduced quantitative features of outbreak data (McBrien *et al.* 1983; Root & Cappuccino 1992). These results suggest that the models describe the biology of this system realistically, and support our hypothesis that food limitation alone can drive insect outbreaks.

Because our main goal has been to establish the plausibility of a general explanation for insect outbreaks, we have focused on simple models. Given that these models provide a closer match to time series of insect outbreaks than do traditional consumer–resource models, it appears that they are realistic enough to be useful (Burnham & Anderson 2002). Moreover, we suspect that including more complicated assumptions would have only a mild effect on our conclusions. For example, because our models' most interesting and realistic behaviours occur when the insect population collapses to low densities, demographic stochasticity could conceivably play a role in plant–herbivore cycles in nature. The state variables in our models, however, are densities per unit area; given that outbreaks often cover very large areas (Liebhold & Kamata 2000), it seems likely that the absolute number of individual insects in nature is large enough that demographic stochasticity is of relatively minor importance.

Similarly, the high degree of synchrony that is typical of many insect outbreaks (Liebhold, Koenig & Bjørnstad 2004) suggests that our models can be useful even though they do not include explicit spatial structure. For the case of the *Trirhabda–Solidago* interaction, however, spatial structure might be expected to be especially important, because at least one *Trirhabda* species, *T. virgata*, increases its emigration rate when defoliation levels are high (Herzig 1995). Nevertheless, our models may be approximately correct at the scale of individual

Solidago stands, because density-dependent emigration is equivalent to the density-dependent death that is already part of the models. More generally, extending the models to allow for spatial structure, including density-dependent dispersal, has confirmed the qualitative results presented here (Abbott 2006).

A final simplifying assumption is that edible plant biomass in a given generation is dependent on the previous year's edible biomass. While this assumption is appropriate for forbs (Bradbury 1981; Hartnett & Bazzaz 1985; Hartnett 1990; Meyer & Schmid 1999), it is not strictly true for woody plants, in that energy stored in the trunk and roots of trees contributes to the production of new edible foliage. Continuous time models can be stabilized completely by a reserve of inedible biomass (Turchin 2003), but simulations show that this is not the case for our models (K.C.A., unpublished data). Although outbreaks appear to occur over a smaller range of parameter values when we modify our models to allow for inedible biomass storage, the models still produce the same range of behaviours as the simpler models presented here. This suggests that our results can be qualitatively correct for outbreaks on woody plants, and Table 1 confirms that outbreaks in forests often show the same temporal pattern of defoliation as outbreaks on forbs.

The long-standing debate surrounding the role of plants in regulating herbivore populations (Hairston *et al.* 1960; Murdoch 1966; Ehrlich & Birch 1967) has been perpetuated by a lack of agreement over what we expect the dynamics of food-limited herbivores to be. In constructing simple models, one of our goals has been to provide quantitative predictions for the behaviour of food-limited herbivore populations with discrete generations. We have thus demonstrated that nonlinearities in food limitation can drive herbivore fluctuations, and that this should be considered as a possible explanation for insect outbreaks. Because our models generate quantitative, testable predictions, our hope is that they can be used by empiricists to identify when food limitation is driving insect outbreaks in nature.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Model parameters used to calculate the ranges of defoliation frequencies given in Table 1.

Appendix S2. Field estimation of *Trirhabda* death rates.

Appendix S3. Parameter estimates for the *Solidago–Trirhabda* system.

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