

Refuge evolution and the population dynamics of coupled host–parasitoid associations

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Summary

We have investigated the theoretical consequences of character evolution for the population dynamics of a host–parasitoid interaction, assuming a monophagous parasitoid. In the purely ecological model it is assumed that hosts can escape parasitism by being in absolute refuges. A striking property of this model is a threshold effect in control of the host by the parasitoid, when host density dependence is weak. The approximate criteria for the parasitoid to regulate the host to low densities are (1) that the parasitoid's maximum population growth rate should exceed the host's and (2) that the maximum growth rate of the host in the refuge should be less than unity. We then use this ecological framework as a basis for a model which considers evolutionary changes in quantitative characters influencing the size of the absolute refuge. For each species, an increase in its refuge-determining character comes at a cost to maximum population growth rate. We show that refuge evolution can substantially alter the population dynamics of the purely ecological model, resulting in a number of emergent and sometimes counter-intuitive properties. In general, when the host has a high carrying capacity, systems are polarized either with low or minor refuge and 'top-down' control of the host by the parasitoid or with a refuge and 'bottom-up' control of the host by a combination of its own density dependence and the parasitoid. A particularly tantalizing result is that co-evolutionary dynamics can modify ecologically unstable systems into ones which are either stable or quasi-stable (with bouts of unstable dynamics, punctuating long-term periods of quasi-stable behaviour). We present five quantitative criteria which must all be met for the parasitoid to be the agent responsible for control of the host at a co-evolutionary equilibrium. The apparent stringency of this full set of requirements supports the empirically-based suggestion that monophagous parasitoid-driven systems should be less common in nature than those driven by multiple forms of density dependence. Further, we apply our theory to the question of whether exploiters may 'harvest' their victims at maximum sustainable yields and to the evolutionary stability of biological control. Finally, we present a series of testable predictions of our theory and methods useful for testing them.

Keywords: co-evolution; parasitoid; population dynamics; refuge; biological control; population stability

Introduction

Substantial evolution can occur over modest time scales (Ford, 1975; Futuyma, 1979) and theoretical studies suggest that small changes in key parameters of population models can have wide ramifications for population behaviour (May, 1976). Since the 1960s (Lewontin, 1968), population biologists have recognized that parameter changes driven by responses to selection could influence population dynamics. Conversely, many evolutionary processes and in particular co-evolution, cannot be clearly understood divorced from an explicit ecological context (Abrams, 1986).

A great deal is now known about the population dynamics of insect host–parasitoid associations, including one host–one parasitoid systems (e.g. Hassell and May, 1973; Murdoch

and Oaten, 1975; Hassell, 1978; Chesson and Murdoch, 1986; Comins *et al.*, 1992; Holt and Hassell, 1993) and multispecies assemblages (Beddington and Hammond, 1977; Hassell, 1978; May and Hassell, 1981; Kakehashi *et al.*, 1984; Hassell and May, 1986; Hochberg *et al.*, 1990; Briggs, 1993; Holt and Lawton, 1993). With rare exception (e.g. Godfray and Hassell, 1991), however, the mathematical theory of host-parasitoid associations has ignored how character evolution can influence the coupled demography of the interacting species. The potential for such evolution has a number of implications for ecological issues, including species invasion, persistence, the nature of population regulation and the effectiveness of biological control.

Since the seminal study of Pimentel (1961) and later Rosenzweig (1973), the theoretical literature on consumer-resource co-evolution has experienced steady growth (e.g. Schaffer and Rosenzweig, 1978; Abrams, 1986; Rosenzweig *et al.*, 1987; Marrow and Cannings, 1993; Saloniemi, 1993; van Baalen and Sabelis, 1993; Frank, 1994; Rand *et al.*, 1994). For instance, Saloniemi (1993) examined the co-evolution of a Lotka-Volterra predator-prey interaction with quantitative genetic characters and showed that the magnitude of additive genetic variances did not influence equilibrium levels, but could profoundly affect stability. van Baalen and Sabelis (1993) considered co-evolution in patch selection by predators and their prey and found that ecologically stable distributions resulted only under restricted circumstances. These studies suggest that evolution can have important implications for population dynamics.

A priori, monophagous parasitoid-host systems would seem particularly likely candidates for analysing the interplay of evolutionary and population dynamics. Populations are often large, permitting the maintenance of large stores of genetic variation and interactions can be very strong, leading to the likelihood of pronounced reciprocal selection. Here we investigate how the evolution of parasitoid attack and host defence characters can influence the coupled dynamics of a single monophagous parasitoid and its host.

It is reasonable to base the co-evolutionary model on an ecological host-parasitoid model in which the parasitoid can persist for at least some parameter values. One broad class of models permitting persistence are those with host refuges (e.g. Rosenzweig and MacArthur, 1963; Hassell and May, 1973; Hassell, 1978; Sih, 1987; Hochberg and Hawkins, 1993). Another factor that promotes persistence is direct density dependence (Hassell, 1978). We begin by defining what we mean by a 'refuge' and present empirical evidence for the existence of proportional refuges. We develop a basic population model incorporating such refuges and direct density dependence and then we expand it to consider evolution of the refuge. Evolutionary dynamics occur in the mean levels of quantitative refuge characters for host and parasitoid. Our results illuminate the reciprocal influences of ecology and evolution in determining the outcome of the host-parasitoid interaction and in particular the likelihood that the host will be limited primarily by the parasitoid.

What is a refuge?

Refuges that can evolve emerge as a consequence of variation in host and parasitoid phenotypes influencing the capacity of parasitoids to parasitize hosts and of hosts to evade parasitism.

Over an individual host's life, it has a certain risk of succumbing to parasitism. This risk is a product of sequential events, each dependent on the external environment and phenotypic characteristics of searching parasitoids and individual hosts. Three major sequential stages in a host-parasitoid interaction can lead to refuges (see also Hassell and Southwood, 1978). First, the *search* stage involves the capacity of the adult female parasitoid to locate a host (Hassell and Southwood, 1978; Waage, 1979; Ayal, 1987). A host's ability to evade being located by the parasitoid may involve morphological or behavioural camouflage, hidden feeding locations

within plant tissues or developmental asynchrony with parasitoids. Second, once a potential host is located, *oviposition* entails the decision by the parasitoid of whether or not to parasitize (e.g. based on host species, size or behavioural defences; Godfray, 1994). The host can evade or escape parasitoid attack using behaviours, noxious chemicals, morphological adaptations or protection within plant tissues. Third, *development* of the larval parasitoid requires the exploitation of the host over some time period as a resource base (Gauld and Bolton, 1988). The host can arrest the attack of the parasitoid larva(e) via physiological immune responses. The population-level concept of 'refuge' thus convolutes multiple aspects of host and parasitoid distributions in space, time and phenotype.

In host-parasitoid systems, refuges can be dynamically important if they generate within-generation heterogeneity in attacks (Chesson and Murdoch, 1986; Hassell and Pacala, 1990). It is useful to describe more fully qualitative features of refuges. Figure 1 presents hypothetical, but

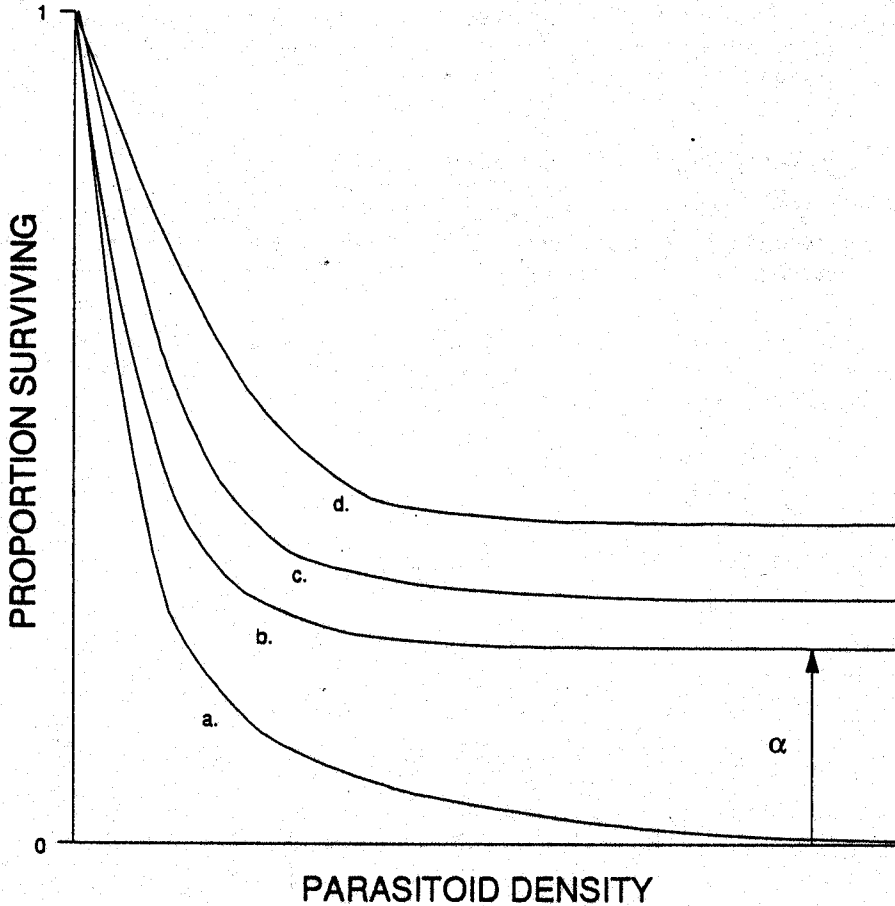


Figure 1. Hypothetical relationship between parasitoid density and the proportion of hosts surviving parasitism from a fixed random sample. In the Nicholson and Bailey model (see Hassell, 1978) where parasitoids search at random, risk approaches unity for all hosts as parasitoid density increases (curve *a*). If there is a positive asymptote in survival as a function of parasitoid density, but host density has no effect on the asymptote (e.g. curve *b* alone), then the host is in a proportional refuge (of size α for curve *b*). If host density influences the asymptote of the relationship (i.e. curves *b*, *c* and *d* each correspond to a different host density) and the proportion of hosts surviving is greater than zero, then a constant-numbers refuge exists.

biologically sensible, relations between parasitoid density and the proportion of a standardized sample of susceptible hosts surviving parasitism in any given generation. In the classical Nicholson–Bailey formulation (see Hassell, 1978), the proportion of hosts escaping parasitism declines asymptotically to zero with increasing parasitoid density (curve a, Fig. 1). Following Hassell (1978), if host density has no effect on the asymptote, then the fraction of hosts corresponding to the asymptotic survival rate are in a *proportional* refuge (e.g. curve b in Fig. 1). By contrast, with a *constant-numbers* refuge, host density will influence asymptotic survival from parasitism (e.g. curves b, c and d in Fig. 1 could represent three different host densities). Both proportional and constant-number refuges are examples of *absolute* refuges – that is, hosts in the refuge are invulnerable to parasitism, irrespective of parasitoid abundance. A complementary way to quantify refuges is to permit variation in survival among hosts, such that certain hosts are at less risk of being parasitized than others (though not necessarily at zero risk). Such hosts can be said to be in *probabilistic* refuges to parasitism (Chesson and Murdoch, 1986; Hassell and Pacala, 1990). In this study, we focus on the evolution of characters contributing to proportional refuges to parasitism, but permit probabilistic refuges to be present and contribute to population stability.

Evidence for proportional refuges

Figure 2 presents the relative frequencies of maximum parasitism rates for 819 native parasitoid assemblages (from Hawkins, 1993). The quantity $1 - \text{maximum parasitism rate}$ (= minimum survival rate from parasitism) is a proxy variable for the proportion of the host population

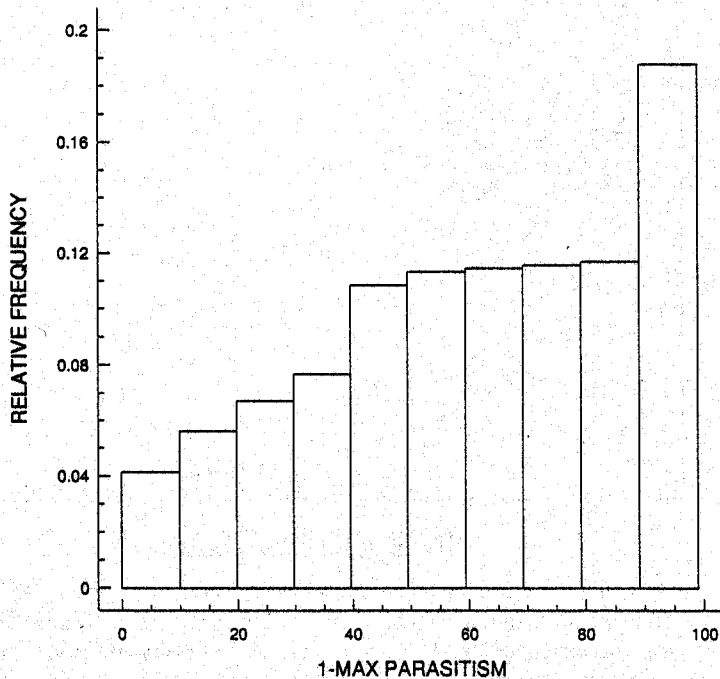


Figure 2. Relative frequency of $(1 - \text{maximum parasitism})$ rates for 819 populations of holometabolous hosts, which provides a proxy variable for the proportion of hosts in the refuge (for details, see Hawkins, 1993; Hochberg and Hawkins, 1994).

found in absolute refuges (i.e. independent of parasitoid density) (for supporting arguments, see Hochberg and Hawkins, 1993, 1994). The data suggest that proportional refuges to parasitism may be widespread in natural communities. For instance, according to Fig. 2, in 96% of host-parasitoid systems at least 10% of the host population seem to be in proportional refuges.

This pattern should be interpreted cautiously for several reasons: (1) systems with low refuge levels may not be reported or observed if hosts are regulated to extremely low numbers (Hochberg and Hawkins, 1992), (2) barring biases in the estimation procedure (van Driesche *et al.*, 1991), the estimated rates will always be less than or equal to the actual maximum rates and (3) Fig. 2 includes full parasitoid assemblages – refuges with respect to individual parasitoid species may tend to be larger.

The refuge levels indicated in Fig. 2 could reflect either reciprocal evolution between the host and its parasitoid(s) (as assumed in the models below) or extrinsic factors (e.g. host plant attributes) or some combination of the two. Nonetheless, these data do suggest at least as a working hypothesis that the evolutionarily stable state of a 'typical' host-parasitoid system may have a substantial fraction of hosts in proportional refuges.

The ecological model

Before presenting the full co-evolutionary model, we must describe the basic ecological model. The discrete, non-overlapping generation model we use combines key elements from a large and growing theoretical literature (e.g. Bailey *et al.*, 1962; Hassell and May, 1973; Murdoch and Oaten, 1975; Hassell, 1978, 1980; May, 1978; May *et al.*, 1981; Hochberg and Lawton, 1990; Holt and Hassell, 1993). An insect host has a density of N_t juveniles at the beginning of generation t and a monophagous parasitoid has a density of female adults of P_t at some fixed time of attack during the host juvenile period. The model is

$$N_{t+1} = \lambda N_t g\{N_t\} (\alpha + (1 - \alpha)f\{N_t, P_t\}), \quad (1)$$

$$P_{t+1} = c N_t g\{N_t\} (1 - \alpha) (1 - f\{N_t, P_t\}) \quad (2)$$

The parameter λ is the largest deterministic rate of increase in the host population in a given environment, here called the 'intrinsic growth rate' or 'basic reproductive rate'. The parameter c is the mean number of adult parasitoid females surviving per parasitized-host and α is the fraction of hosts invulnerable to parasitism (i.e. in the proportional refuge).

Equations 1 and 2 are characterized by two further functions, each of which encapsulate realistic biological phenomena in a simple mathematical expression.

First, the function $g\{N_t\}$ is the proportion of hosts escaping density-dependent mortality. There are a number of ways in which $g\{N_t\}$ can be modelled (Hassell, 1978) and its functional form can have important influences on population dynamics (Hassell, 1975, 1978; Hochberg and Lawton, 1990). Our aim being to explore how a single species of parasitoid may influence the dynamics of its host, a logical starting point is to assume that the host population is self-regulated at a stable equilibrium in the absence of the parasitoid and to see how the parasitoid may or may not disrupt the system. The function we employ is

$$g\{N_t\} = [1 + N_t(\lambda - 1)/K]^{-1} \quad (3)$$

where the constant K is the carrying capacity of the host population. This model describes compensatory, stabilizing density dependence (Hassell, 1975), such that the host population

monotonically approaches K in the absence of the parasitoid. We assume $\lambda > 1$ and $K > 0$, ensuring host persistence without the parasitoid.

Second, the function $f\{N_t, P_t\}$ is the proportion of juvenile hosts outside the refuge that survive parasitism. The functional form we use has a long pedigree (e.g. Bailey *et al.*, 1962; May, 1978; Hassell, 1980; Kekehashi *et al.*, 1984; Chesson and Murdoch, 1986; Perry and Taylor, 1986). In our version, we assume all parasitoids can potentially attack any host outside the refuge and do not waste time trying to attack protected hosts.

$f\{N_t, P_t\}$ is given by

$$f\{N_t, P_t\} = \left[1 + \frac{aP_t}{k(1 + aN_t g\{N_t\} (1 - \alpha)/\eta)} \right]^{-k} \quad (4)$$

where a is the parasitoid 'searching efficiency', k is the clumping parameter of the negative binomial distribution (a measure of probabilistic refuges to parasitism independent of host density; Chesson and Murdoch, 1986) and η is the maximum number of hosts attackable per female parasitoid (when the $Ng(1 - \alpha)$ hosts susceptible to parasitism are sufficiently numerous). Note that if $\eta \rightarrow \infty$, the expression reduces to the ordinary negative binomial, which ensures strict stability if $k < 1$, in the absence of other forms of density dependence (Hochberg and Lawton, 1990). The functional form of Equation 4, though complex, does include key aspects of parasitism known to be dynamically significant, such as the aggregation of parasitoid searching effort (reflected by k) (May, 1978; Hassell, 1980; Chesson and Murdoch, 1986) and limitations in the number of hosts a parasitoid can attack (parameterized here as η) (Hassell, 1978, 1980).

An explicit assumption of our model which should be noted is that self-limitation in the host population ($g\{N_t\}$) acts at an earlier stage in the host's life-cycle than does parasitism ($f\{N_t, P_t\}$), so that parasitism is inflicted only on those hosts surviving density dependence. Other orderings of density-dependent factors are possible and they each can have different ramifications for host population dynamics (May *et al.*, 1981). We leave the analysis of alternative models with different life-history assumptions for future study.

Parasitoid invasion

In this model, the basic reproductive rate of the host is simply a parameter, λ , whereas the parasitoid's basic reproductive rate, denoted as R_0 , is more complex, in that it is determined by host availability. We define R_0 to be the number of egg-laying, female adults produced by a single fecund female adult introduced into a parasitoid-free host population. If $R_0 > 1$, the parasitoid deterministically invades.

R_0 is the ratio P_{t+1}/P_t evaluated in the limit $P_t \rightarrow 0$ with the host at arbitrary density N_0 ,

$$R_0 = \frac{c\eta}{1 + \eta/(aN_0 g\{N_0\} (1 - \alpha))} \quad (5a)$$

R_0 increases with the number of susceptible hosts ($N_0 g\{N_0\} (1 - \alpha)$), parasitoid searching efficiency (a), parasitoid survival within parasitized hosts (c) and the maximum number of hosts attackable per parasitoid (η). $R_0 \approx c\eta$ when non-refuge hosts are sufficiently abundant and the host is not limited to invading parasitoids (i.e. $K \rightarrow \infty$). This quantity in effect is the intrinsic population growth rate for the parasitoid, when hosts (after density dependence) are super-abundant.

The parasitoid basic reproductive rate R_0 reflects both intrinsic and extrinsic factors. The numerator is proportional to the parasitoid's intrinsic population growth rate, while the denominator discounts this based on actual host availability. It may not be intuitively obvious

why the level in spatial heterogeneity in parasitism, measured by k , has no effect on parasitoid invasion. The reason is that the functional form of Equation 4 implicitly assumes that at low parasitoid densities (e.g. early in a parasitoid invasion) parasitoid offspring do not compete, nor does patchiness in the host distribution affect the ability of a parasitoid to locate hosts.

If the parasitoid invades when the host is at equilibrium ($N' = K$), then

$$R_{N'} = \frac{c\eta}{1 + \eta\lambda/(aK(1 - \alpha))} \quad (5b)$$

Because increasing λ lowers pre-parasitism host survival (via $g\{N_t\}$), the basic reproductive rate of the parasitoid decreases with increasing host productivity λ ; however, this effect is quantitatively important only when the total number of hosts available for parasitism is of the same order or less than the intrinsic attack rate of the parasitoid (i.e. $\eta \geq aK(1 - \alpha)/\lambda$).

Numerical simulations

Except for some special limiting cases, we were not able to derive readily interpretable, transparent analytical expressions for the dynamics of the system (e.g. one cannot usually write down closed-form solutions for the two-species equilibrium). We therefore studied the model with numerical simulations. We introduced the parasitoid at very low densities (i.e. $P_0 = 1.1 \times 10^{-6}$) into a system with the host at carrying capacity and iterated the model until either (1) the host and/or parasitoid population dropped below an arbitrary density of 1.0×10^{-6} (i.e. 'extinction'), or (2) both μ host and parasitoid populations did not change by more than 10^{-10} of their values for 25 consecutive generations ('stable two-species equilibrium'), or (3) conditions (1) and (2) were not met for more than 50 000 generations ('two-species cycles') (we do not distinguish types of cyclic behaviour (e.g. chaos) in this study).

Using data from Hassell (1978) and Hassell and Pacala (1990) as guidelines, a set of baseline parameter values was selected as a reference in the numerical simulations (Table 1). λ and η were assigned identical intermediate values of 10 and k an intermediate value of 0.9. The host carrying

Table 1. Baseline parameter values and initial conditions employed in this study

Parameter	Symbol	Value
Intrinsic growth rate of host	λ	10
Host carrying capacity	K	1E7
Intrinsic attack rate of parasitoid	η	10
Survival of parasitoid larvae	c	1
Parasitoid searching efficiency	a	1
Spatial heterogeneity in parasitism	k	0.9
Proportional refuge to parasitism	α	0
Additive genetic variance in host	Γ_n	0.01
Additive genetic variance in parasitoid	Γ_p	0.01
Cost to host character	C_n	1
Cost to parasitoid character	C_p	1
Inflection to refuge function	s	1
Initial host density	N_0	K
Initial parasitoid density	P_0	1.1E-6
Initial host character	\bar{n}_0	1
Initial parasitoid character	\bar{p}_0	0

capacity, K , was set to a high value of 10^7 and the rate of parasitoid survival within parasitized hosts, c , and the parasitoid search rate, a , were each set to unity. Finally, we assume no proportional refuge (i.e. $\alpha = 0$). These baseline parameter choices imply $R_0 = \eta$ and result in a locally stable host-parasitoid equilibrium.

Outcomes

Starting at these reference values, we explored a broad range of parameter spaces. The model outcomes broadly match those observed in previous studies (Bailey *et al.*, 1962; Hassell and May, 1973; Murdoch and Oaten, 1975; Hassell, 1978, 1980; May, 1978; May *et al.*, 1981; Hochberg and Lawton, 1990; Holt and Hassell, 1993). Four qualitative outcomes can be identified (Fig. 3).

(1) *Host and parasitoid persist at a locally stable equilibrium.* Sufficiently high λ and low k always result in a single, locally stable equilibrium point enforced by the parasitoid (Fig. 3a), denoted N^* , P^* . Even minute amounts of refuge, α , can confer substantial stability (Fig. 3b) and when $\alpha\lambda > 1$, the system is always stable. The stabilizing effects of increased λ and α are due to control in the system shifting from domination by the parasitoid (which, with $k = 0.9$, is at the limit of being stabilizing on its own; May, 1978) to stabilizing contest competition in the host (Hassell, 1975).

(2) *Host and parasitoid persist with cyclic dynamics.* Moderate λ and k (but, $k > 1$) lead to persistent cycles around an unstable two-species equilibrium point (Fig. 3a). The parameter space resulting in such cycles was found to be greatest for $\lambda \approx \eta$ and no proportional refuge (Fig. 3b).

(3) *Parasitoid goes extinct.* If the absolute refuge is either very small or absent, decreasing spatial heterogeneity (i.e. $k \gg 1$) invariably leads to parasitoid extinction because of expanding oscillations (and the parasitoid population falling below the arbitrary extinction threshold) (Fig. 3a and b). The parameter space permitting parasitoid extinction increases as $\eta \rightarrow 1$ (not shown), or when the parasitoid is on the edge of extinction regardless of host dynamics.

(4) *Host and parasitoid go extinct.* Still lower levels of spatial heterogeneity result in the extinction of both host and parasitoid (Fig. 3a), following expanding cycles and a numerical underflow. This requires, as for case (3), that $\alpha \rightarrow 0$ (Fig. 3b).

Host depression and system resilience

The host is ensured of persisting in the face of an otherwise destabilizing parasitoid if a sufficient refuge exists (see Fig. 3b). When the carrying capacity K of the host is sufficiently large, a striking property of the ecological model is a clean demarcation in the levels of the parasitoid-enforced equilibrium of the host (measured by $q = N^*/K$ (Beddington *et al.*, 1975), where N^* is the equilibrium level of hosts as depressed by the parasitoid) depending on the host intrinsic growth rate (Fig. 4a-c). For $\lambda > \eta$ the parasitoid's impact on the host population can be *several orders of magnitude* less severe than for $\lambda < \eta$. However, when the carrying capacity of the host is sufficiently small, this threshold phenomenon all but disappears.

To highlight these contrasting actions of the parasitoid, it is instructive to identify systems as either (1) highly depressed by the parasitoid (i.e. $q \ll 1$) or under 'top-down control', (hereafter abbreviated 'TD') or (2) moderately to slightly depressed (i.e. $0.1 \leq q < 1$) or under 'bottom-up control' ('BU'). (We use the TD-BU dichotomy to distinguish the contrasting levels of control by the parasitoid and do not mean to suggest that the parasitoid has no impact at all on the host in the case of BU control). A similar threshold effect on parasitoid-enforced host density occurs as a function of refuge level, such that when $\alpha\lambda > 1$ the control is BU, whereas when $\alpha\lambda < 1$ control can be, but is not necessarily, TD (Fig. 4c; see also Hochberg and Hawkins, 1993, 1994). In

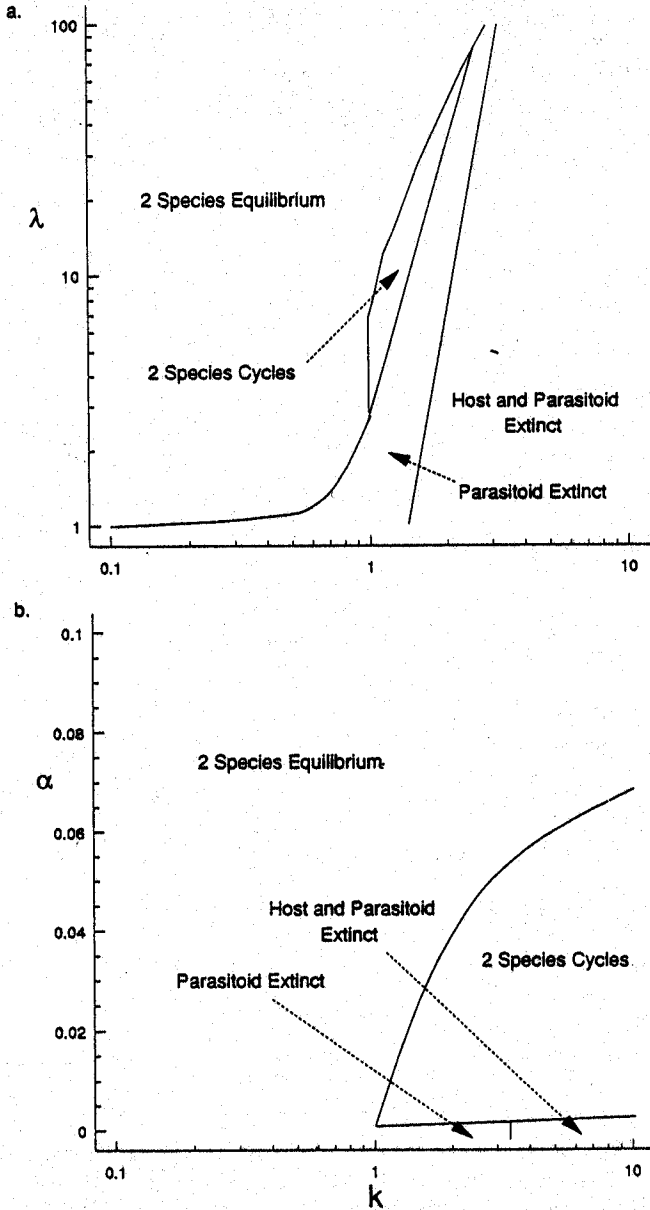


Figure 3. Outcomes of the host-parasitoid interaction for the ecological model. (a) The joint effects of spatial heterogeneity (k) and host intrinsic growth rate (λ). (b) The joint effects of k and the proportion of hosts in the refuge (α).

effect, when $\alpha\lambda > 1$ the proportion of hosts in the refuge is sufficiently large to grow until directly checked by density dependence.

The threshold can be expressed mathematically by examining the conditions for host regulation by the parasitoid. For analytical simplicity, let $\alpha = 0$, $k = 1$, $c = 1$, and $a = 1$. The equilibrium level of the host is determined implicitly by

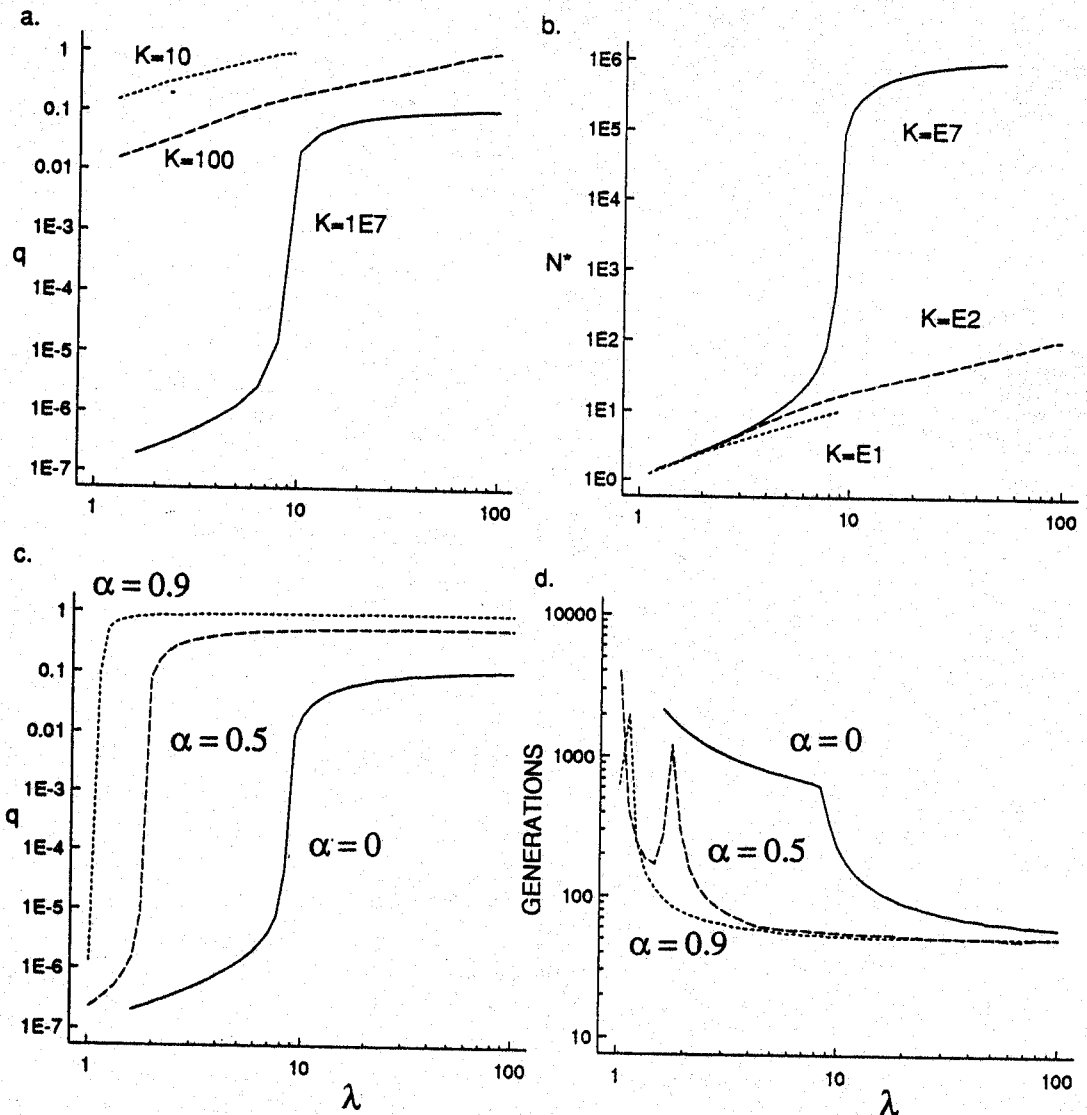


Figure 4. Effect of key parameters on the stable host-parasitoid equilibrium. Effect of host carrying capacity (K) on (a) host population depression (q) and (b) host density (N^*). Effect of proportional refuge level on (c) host population depression (q) and (d) the number of generations required to achieve equilibrium (using numerical criterion specified in the text).

$$N^* = \frac{1}{1/\lambda - g\{N^*\}/\eta} \quad (6)$$

In the limit $K \rightarrow \infty$ the parasitoid is the only potential regulatory agent of the host; $g \approx 1$ and the parasitoid regulates the host only if $\eta > \lambda$. Increasing η decreases N^* and as $\eta \rightarrow \infty$ (i.e. the risk of parasitism is independent of host density) the parasitoid depresses the host to $N^* = \lambda$. If $\eta < \lambda$ then the host population grows unregulated (see also Hassell, 1978), so this is BU control. The precision of this condition for the direction of control is lost as $\lambda \rightarrow K$ or, in other words, as

the host's carrying capacity approaches densities below which the parasitoid population cannot, in any case, persist.

Figure 4d shows how λ and α affect the resilience of the system, measured as the number of generations to attain the stability criteria (see above). In general, increasing host productivity or the level of the refuge, either separately or together, decreases times to the equilibrium (i.e. increases resilience). There is a blip in the region of the threshold between TD and BU systems. (We do not yet understand why these particular trajectories near the switch take so much longer to reach equilibrium.)

The co-evolutionary model

The above results all assume constant parameters. However, given the sensitivity of the ecological model's properties to parameter changes (Figs 3 and 4), the patterns produced could break down when some of the phenotypic characters influencing the parameters can evolve. The co-evolutionary model we now develop incorporates reciprocal selection on a pair of refuge-determining phenotypic characters.

The refuge function

We assume that the absolute refuge depends on a single character in each species, denoted n and p for the host and parasitoid, respectively and, in particular, that the fraction, α , of hosts escaping parasitism is determined as a function of the mean phenotypes of both species, $\alpha\{\bar{n}, \bar{p}\}$. A more general treatment would replace this with explicit functions, indicating how each phenotypic class in one species interacts with all classes in the other (e.g. Frank, 1994). We leave this for future work. Specifically, we here take a phenomenological approach to refuge evolution by assuming the fraction of hosts invulnerable to parasitism is a sigmoidal function of the difference in the mean phenotypic characters, \bar{n} and \bar{p} (with both \bar{n} and $\bar{p} \geq 0$). The sigmoidal function is used as an approximation of a cumulative normal distribution in the host phenotypes escaping parasitism due to the proportional refuge. This scenario implies that the refuge results from a modified truncation selection process (Roughgarden, 1979), such that only sufficiently extreme host phenotypes are invulnerable to parasitism.

The proportion of hosts in the refuge in generation t is

$$\alpha_t\{\bar{n}_t, \bar{p}_t\} = 1 - \exp\{-s(\bar{n}_t - \bar{p}_t)^2\} \quad (7)$$

with the constraint $\bar{n}_t \geq \bar{p}_t$; if $\bar{p}_t > \bar{n}_t$, we assume that small amounts of directional selection on the parasitoid act to keep the mean parasitoid character from exceeding that of the host. In what follows, \bar{n} and \bar{p} are scaled such that $s = 1$. Equation 7 implicitly assumes that the host and parasitoid characters are measured on commensurable scales (e.g. ovipositor length in the parasitoid and depth of egg or larval placement by the host within plant tissues; both characters have the dimension 'length').

Evolution of phenotypic means

The recursion equations we use to describe how mean phenotypes change from generation t to $t + 1$ are standard quantitative genetic formulations for phenotypic evolution (Lande, 1976). The characters are assumed to have distributions with constant variance; the quantities Γ_n and Γ_p are additive genetic variances for the host and parasitoid, respectively and are assumed to be constant. The assumption of constancy is most appropriate if there is weak selection and if mutation rates are sufficient to replenish genetic variation (Lande, 1976; Roughgarden, 1979; see

Turelli and Barton (1994) for justification). The evolutionary component of the full model is as follows

$$\bar{n}_{t+1} = \bar{n}_t + \Gamma_n \left[\frac{\partial \ln \bar{W}_n}{\partial \bar{n}} \right] \quad (8a)$$

$$\bar{p}_{t+1} = \bar{p}_t + \Gamma_p \left[\frac{\partial \ln \bar{W}_p}{\partial \bar{p}} \right] \quad (8b)$$

Here, $\bar{W}_n = N_{t+1}/N_t$ and $\bar{W}_p = P_{t+1}/P_t$ are the fitnesses of the host and parasitoid, respectively, described by Equations 1 and 2, with Equation 7 substituted for α . At an evolutionary equilibrium, it must be the case that for the host, $\partial \ln \bar{W}_n / \partial \bar{n} = 0$ and for the parasitoid, $\partial \ln \bar{W}_p / \partial \bar{p} = 0$; each character must be at a local optimum.

Costs of character evolution

An increase in the mean phenotypic character of the host, \bar{n} , is assumed to entail an immediate and direct cost ($C_n \bar{n}$) to the (maximum) cost-free, intrinsic population growth rate, denoted λ^* , such that the host's realized intrinsic growth rate in generation t is

$$\lambda_t\{\bar{n}_t\} = \lambda^* - C_n \bar{n}_t \quad (9a)$$

(It is necessary to interpret the parameter λ within g (Equation 3) either as the cost-free, intrinsic growth rate λ^* or as the current rate λ_t . So as not to confound refuge evolution with density-dependent survival, we assume $g\{N_t, \lambda^*\}$.)

For the parasitoid, the cost of character growth could be expressed via several parameters: the searching efficiency (a), the within-host survival rate (c) or the intrinsic attack rate (η). Here, we assume the latter, because it can be interpreted in the same units as λ (namely, offspring produced). The cost-free, intrinsic attack rate of the parasitoid, $\eta^* = \eta$ is reduced to the realized attack rate as follows

$$\eta_t\{\bar{p}_t\} = \eta^* - C_p \bar{p}_t \quad (9b)$$

at generation t .

The full co-evolutionary model is specified by Equations 1 and 2 for changes in the host and parasitoid population sizes and indirectly of \bar{n} and \bar{p} via Equations 8a and 8b, Equation 7 for determining the relation between character values and refuges size, Equations 8a and 8b for determining evolution in character values and Equations 9a and 9b for giving λ and η .

Numerical simulations

The model is complex and, except for special limiting cases, must be analysed numerically. The results presented below provide a synoptic overview of a large number of simulations. Unless otherwise specified, we followed the protocol sketched above for the ecological model, with the exception that at the beginning of each simulation the refuge character of the host was always positive (i.e. $\bar{n}_0 > 0$, but $\bar{p}_0 = 0$). We assume an initial small level of refuge because the structure of the refuge function implies the refuge never evolves if $\bar{n}_0 = 0$ (because in this case, the selection gradient (a linear approximation of a more complicated Taylor series expansion) in Equation 8a is negative). The other baseline parameter values used are those given in Table 1.

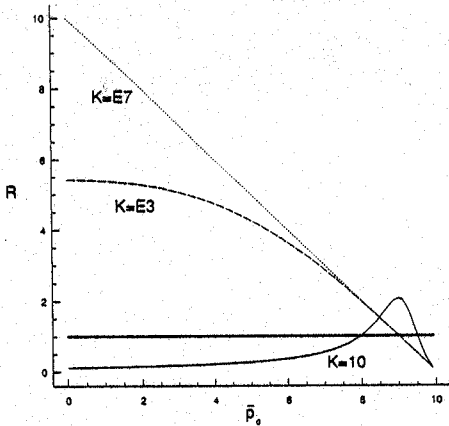


Figure 5. Influence of the initial value of the parasitoid character (\bar{p}_0) and the host carrying capacity (K) on the invasion criterion for the parasitoid. Cases of $R_0 > 1$ (above bold line) correspond to successful invasion. Initial refuge level: $\alpha_0 = 0.1$.

Parasitoid invasion

To highlight the importance of the trade-off between the parasitoid's ability to exploit refuge hosts ($1 - \alpha_t$) and its intrinsic attack rate (η_t), consider the case where the parasitoid attempts to invade given a host population at carrying capacity, $N' = K$. Invasion is successful if $R_{N'} > 1$ or

$$\frac{c\eta_0}{1 + \eta_0\lambda_0/(aK(1 - \alpha_0))} > 1 \tag{10}$$

With no extrinsic constraints on invasion (i.e. host K large), because $\eta_0 = \eta^* - C_p\bar{p}_0$, increasing the ability of the parasitoid to exploit maximally the host population (via increased \bar{p}_0) always *reduces* the capacity of the parasitoid to invade. With extrinsic constraints, the effect of increasing \bar{p}_0 is less apparent. Figure 5 shows that for sufficiently low K , the maximum $R_{N'}$ occurs at *intermediate* levels of \bar{p}_0 ; either too small or too large an initial character can result in a failed invasion. Too small a \bar{p}_0 means that any refuge is sufficient, in conjunction with low K , to push $R_{N'}$ below unity; too large a \bar{p}_0 results in insurmountable costs on the intrinsic attack rate of the parasitoid. Therefore, extrinsic resource limitation on the host can play an important role in determining which parasitoid phenotypes can invade.

Patterns in refuge evolution

Refuge evolution leads to new patterns in dynamical outcomes as compared to the ecological model (e.g. cf. Figs 3a and 6d). Put concisely, the refuge tends to evolve (generally ensuring stable host - parasitoid persistence and a host population not depressed far below its K) for (1) high $\lambda^* : \eta^*$ and/or $C_p : C_n$ ratios, (2) intermediate η^* , (3) high K and (4) high k . We consider these effects in turn below.

(1) **High host growth to cost ratio.** For the refuge to evolve such that the system attains a locally stable equilibrium, the host must have a sufficient residual capacity for population growth, once costs for the refuge are deducted (Fig. 6a). Due, in part, to the assumed linear form of such costs (Equations 9a and 9b), the threshold for refuge evolution is approximately linear, too, as long as C_n is not too large (Fig. 6a); for small deviations from the baseline parameter set, the approximate condition for refuge evolution is $\lambda^*/C_n > \eta^*/C_p$. For C_n sufficiently large compared

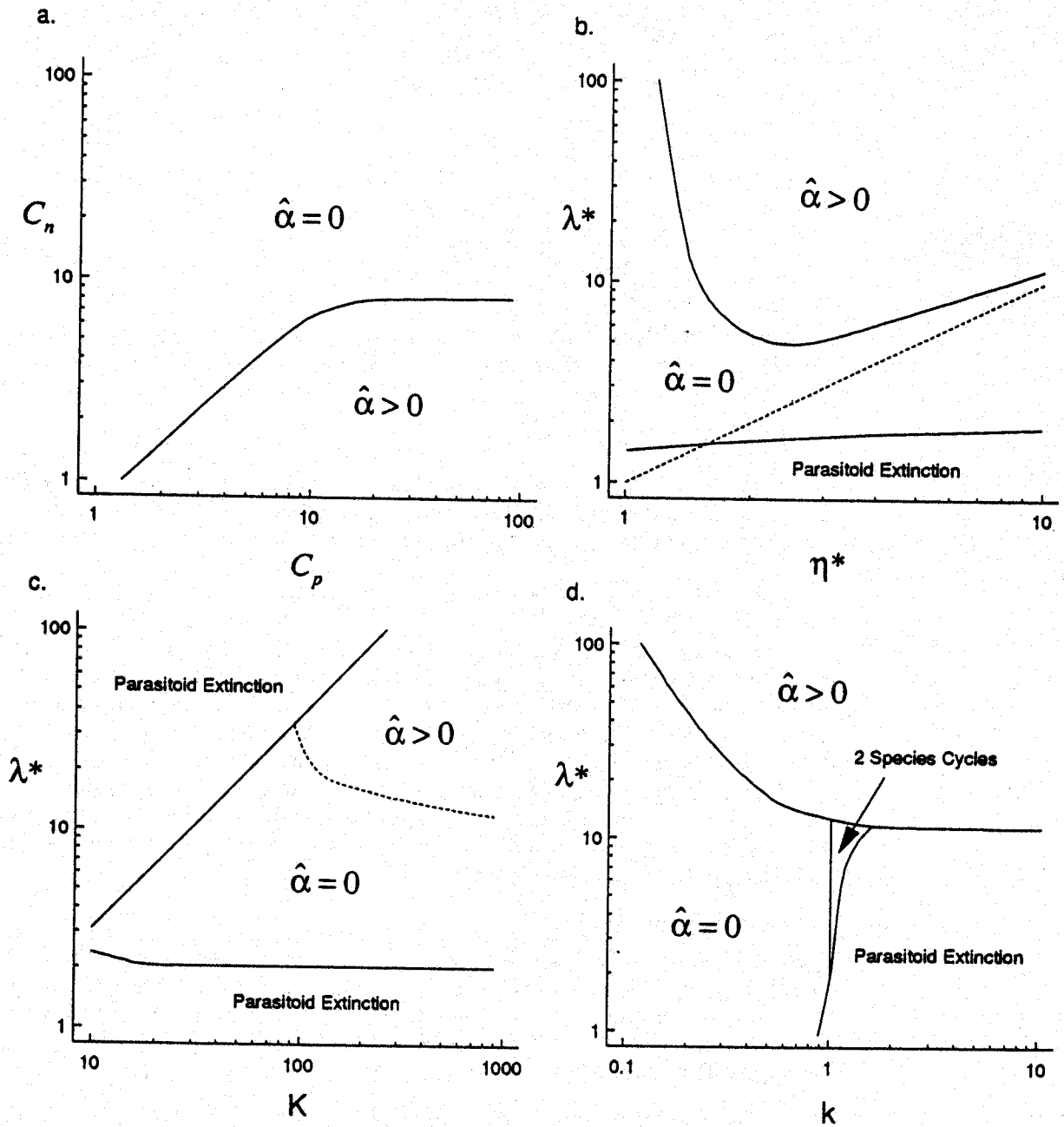


Figure 6. Refuge evolution based on (a) unit costs (with $\bar{n}_0 = 1/C_n$), (b) levels of η^* and λ^* (dotted line corresponds to a 1 : 1 relationship), (c) host carrying capacity, K (the lower refuge boundary (dotted line) corresponds approximately to the ecological TD-BU threshold) and (d) the level of spatial heterogeneity, k .

to λ^* (ca. $C_n = 10$ in Fig. 6a), the refuge never evolves due to its costliness to the host. For the special case $C_n = C_p$ (with both sufficiently small), the boundary for refuge evolution corresponds approximately to the ecological TD–BU interface; with a refuge the system is BU, without it, the system tends to be TD.

(2) **Intermediate η^* .** The evolutionary persistence of the refuge depends on the absolute level of the parasitoid's intrinsic attack rate, η^* (Fig. 6b). All else being equal, the minimum $\lambda^* : \eta^*$ ratio necessary for refuge evolution approaches unity as η^* increases. For any fixed set of parameters, an intermediate η^* is most likely to yield an evolutionarily persistent refuge. This is because at very small η^* the selection pressure of the parasitoid is insufficient to maintain a host refuge for all but very large λ^* . At very high η^* relative to λ^* , the parasitoid experiences little cost in countering any refuge evolution by the host and so can prevent refuge evolution.

(3) **High host carrying capacity.** The carrying capacity of the host must be sufficiently large for the refuge to be evolutionarily persistent (Fig. 6c). When K is too low relative to λ^* , host density after self-limitation ($g\{N, \lambda^*\}$) has acted is not large enough for the parasitoid to persist; clearly, there can be no selection for a refuge if the parasitoid is absent. As K is increased, a band yielding persistent systems with no refuge emerges at intermediate λ^* ; basically, these persistent parasitoid populations only occur for levels of λ^* too low to permit refuge evolution (see Fig. 6b). For sufficiently high K and λ^* , a second band emerges yielding systems with $\hat{\alpha} > 0$.

(4) **Low spatial heterogeneity.** Increasing the level of spatial heterogeneity in the system, as mentioned before, decreases the propensity of the refuge to evolve (Fig. 6d). The negative relation between spatial heterogeneity (a probabilistic refuge) and the evolution of the proportional refuge is intriguing, for it suggests that the existence of one 'refuge type' may impede evolution of the other.

Effect of population growth rates

Figures 7a and b illustrate threshold effects in refuge evolution. When λ^* is just sufficient for the refuge to persist, the parasitoid character always evolves to reduce the refuge, as long as the cost-free, intrinsic attack rate (η^*) is sufficiently large and the per unit character cost (C_p) sufficiently small. As λ^* is increased past the threshold (approximately 10 in Fig. 7), the parasitoid is increasingly constrained in its ability to 'keep-up' with the host, such that as λ^* increases, $\hat{\lambda} \rightarrow \lambda^*$, $\hat{\eta} \rightarrow 1$ and $\hat{\alpha} \rightarrow 1$ (where the 'hat' symbol refers to the co-evolutionary equilibrium).

Previous studies have highlighted the importance of the portion of overall host growth rate stemming from individuals within the refuge in determining population dynamics (Hassell, 1978; Perry and Taylor, 1986; Hochberg and Hawkins, 1992, 1993; Holt and Hassell, 1993). Analysis of the co-evolutionary model shows that, for large host carrying capacity, it is only in the narrow region corresponding to the shift from non-refuge to refuge systems where the intrinsic growth rate of the host within the refuge is greater than zero, but less than unity (i.e. $0 < \hat{\alpha} \hat{\lambda} < 1$) (Fig. 7c). This suggests that many real systems may be polarized, such that hosts are either potentially regulated by the parasitoid (with $\hat{\alpha} = 0$) or dominated by other forms of density dependence (because $\hat{\alpha} \hat{\lambda} > 1$ allows the host to grow until it is regulated by other factors).

Alternative outcomes and system resilience

Whereas moderate deviations from the baseline initial host and parasitoid densities had no effect on outcomes in numerical simulations of the purely ecological model, the particular equilibrium achieved in the co-evolutionary model (i.e. either $(\hat{N}, \hat{P}, \hat{n}, \hat{p})$ or $(\hat{N}, \hat{P}, 0, 0) \equiv (N^*, P^*)$) often does depend on additive genetic variances and the initial refuge character levels.

At sufficiently low \hat{n}_0 the host decreases its refuge character to zero. In the example shown in Fig. 8, the initial refuge level alone (\hat{n}_0) can determine whether (1) the refuge evolves at all

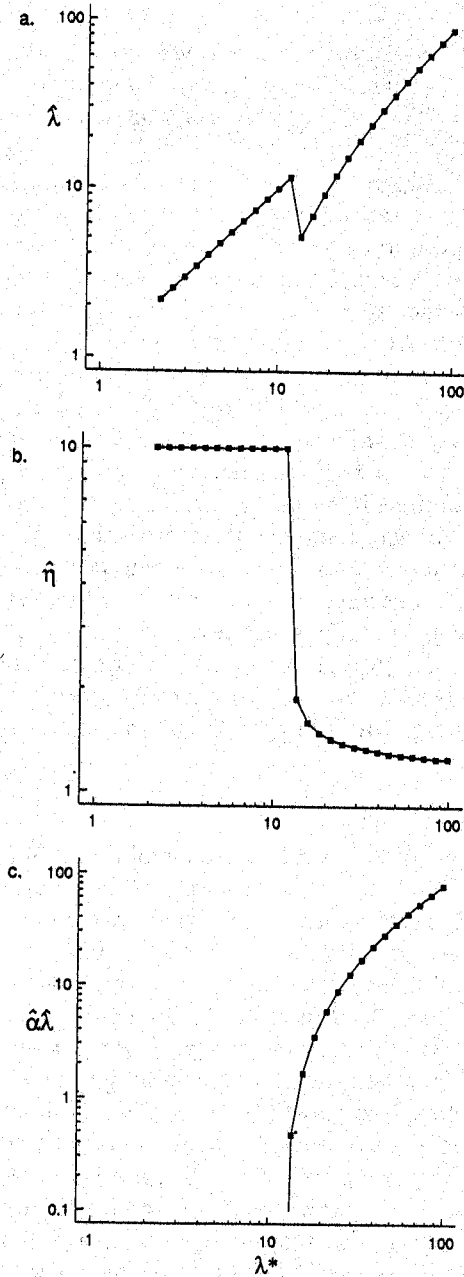


Figure 7. Effect of cost-free, intrinsic host population growth rate (λ^*) on (a) the equilibrium intrinsic host growth rate ($\hat{\lambda}$), (b) the equilibrium intrinsic parasitoid attack rate ($\hat{\eta}$) and (c) the equilibrium growth rate ascribable to the host subpopulation in the refuge ($\hat{\alpha}\hat{\lambda}$).

(points *a* or *b*), (2) a system is cyclic or locally stable (*c* or *b*), (3) the parasitoid becomes extinct or cyclic populations ensue (*e* or *d*) or (4) both species or only the parasitoid becomes extinct (*f* or *e*). More generally, because sufficiently (but not too) high \bar{n}_0 was found to be associated with the evolution of the refuge, a large initial refuge character can be said to generally permit greater

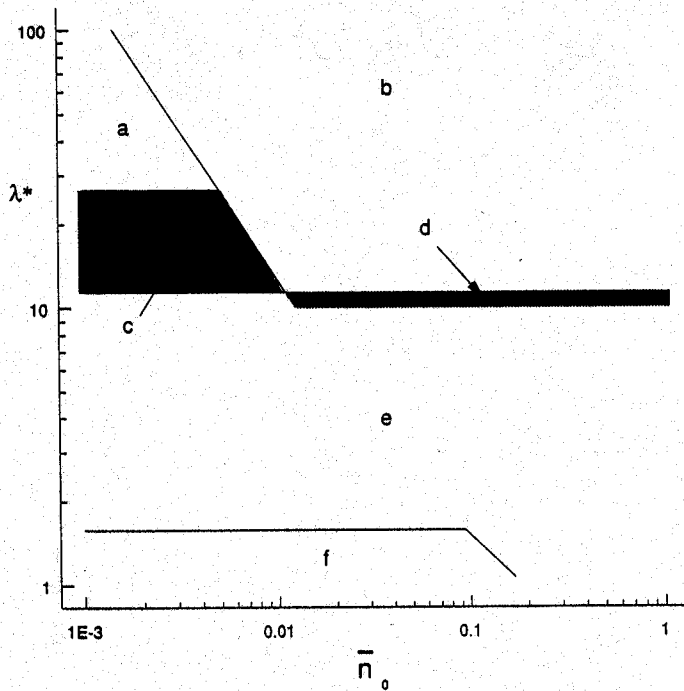


Figure 8. Outcomes based on the initial host character level (\bar{n}_0) and the cost-free, intrinsic host growth rate (λ^*). (a) Locally stable two species equilibrium with $\hat{\alpha} = 0$, (b) locally stable two species equilibrium with $\hat{\alpha} > 0$, (c) two species persistent cycles with no refuge evolution, (d) two species persistent cycles with refuge evolution, (e) parasitoid extinct and (f) host and parasitoid extinct. Parameters as for Table 1, except $k = 1.5$.

persistence and/or population stability. Hosts which initially have a low to zero level of refuge may be evolutionarily 'trapped' in that state.

The potential rate of host character evolution is governed by genetic variance (Γ_n) and can also influence which of the two locally stable equilibria is achieved (not shown). Somewhat counter-intuitively, increasing Γ_n promotes the attainment of an ecological equilibrium without a refuge ($\hat{N}, \hat{P}, 0, 0 \equiv N^*, P^*$). This is because large Γ_n yields large transients in \bar{n}_t ; we generally observed the dominance of the ecological equilibrium (at $\bar{n}_t = 0$) as a stable attractor in systems with such fluctuating phenotypes.

The times required for the system to attain a steady state increase, given a tendency for refuge evolution to occur (i.e. with decreasing C_n and increasing λ^*). Note, that whereas higher λ resulted in greater resilience in the purely ecological model, higher λ^* results in *decreased* resilience in the co-evolutionary model. Thus, permitting co-evolution increases the time scale over which attainment of an ecological equilibrium must be assessed.

Illustrative examples

A series of four examples illustrates how passing from ecological 'top-down' to 'bottom-up' systems can influence the coupled evolutionary and population dynamics when the two-species equilibrium point of the basic ecological model is, on its own, locally unstable (Fig. 9). The only

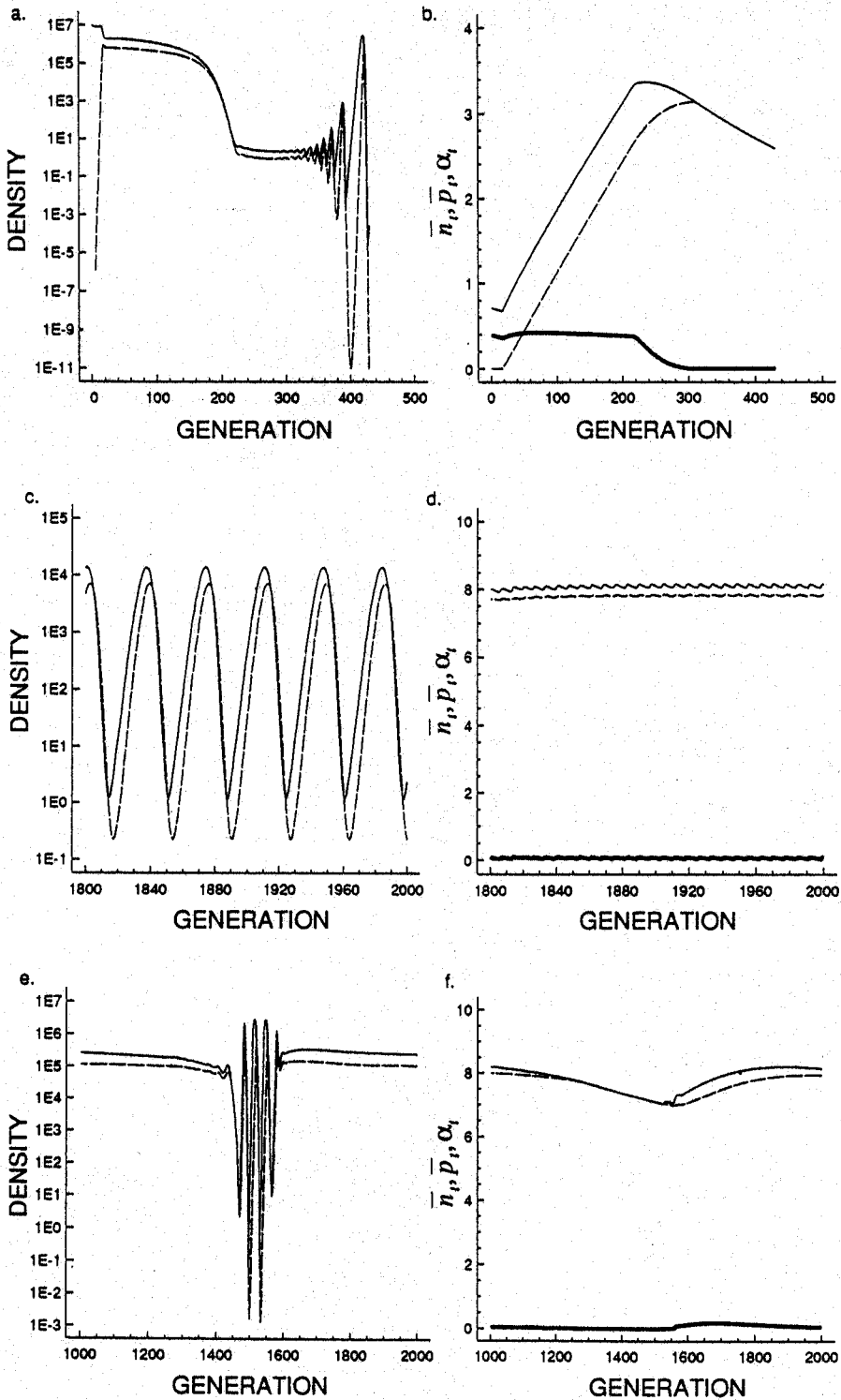


Figure 9a-f.

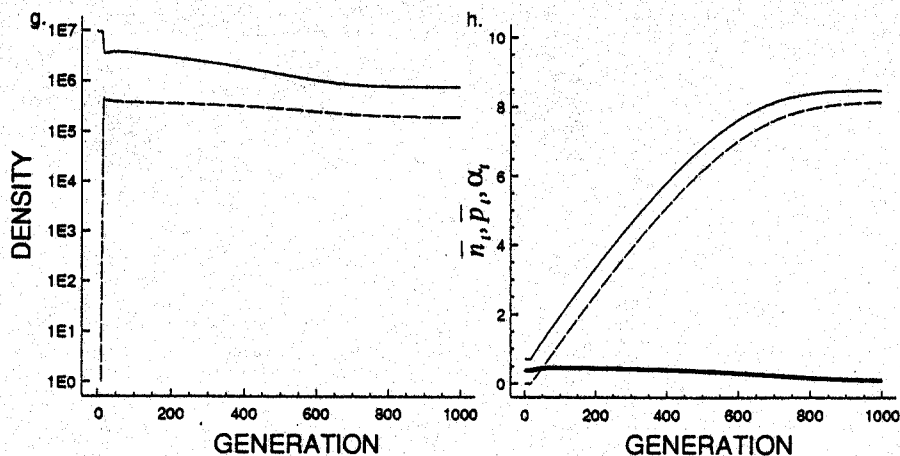


Figure 9. Population, character and refuge dynamics resulting from different values of the cost-free, intrinsic population growth rate of the host. (a,b) $\lambda^* = 5$, (c,d) $\lambda^* = 10$, (e,f) $\lambda^* = 11$, (g,h) $\lambda^* = 12$. Solid lines refer to host character, broken lines to the parasitoid character and thick lines to the proportional refuge (determined jointly by both characters). Parameters as for Table 1, except $k = 1.5$.

parameter changing among these examples is the host's (maximal) intrinsic growth rate, λ^* . We assume \bar{n}_0 sufficiently large to permit refuge evolution (see Fig. 8b).

Example 1: $\lambda^* = 5$

For the first approximately 200 generations of the simulation, the parasitoid depresses the host (Fig. 9a) and the refuge characters evolve in tandem with little effect on the overall refuge level (Fig. 9b). However, once the populations assume the quasi-equilibrium levels characterizing the TD nature of the interaction, the refuge character of the parasitoid 'catches-up' to the host and the instabilities associated with the pure ecological model begin to dominate the dynamics. For the remaining 100 or so generations the oscillations expand until the parasitoid goes extinct. During this unstable period the levels of the refuge characters begin to de-evolve, but not completely. Following parasitoid extinction, the host eventually achieves K and its refuge character would shrink to zero were the simulation continued. The parasitoid could then reinvade if introduced in small numbers, as would be feasible in a metapopulation. A parasitoid may persist in a metapopulation if local colonization matches local extinction. Our theoretical results highlight the potential role of local co-evolution in determining local extinction rates.

Example 2: $\lambda^* = \eta^* = 10$

When increasing λ^* from TD control up to the TD-BU interface, after approximately 1000 generations, the system shows sustained population and character oscillations, with the realized refuge level hovering just above zero (Figs 9c and d). In the example shown, parasitoid abundance fluctuates over almost five orders of magnitude every 15 or so generations (Fig. 9c). In contrast, the refuge character oscillations are minute in magnitude, with a much smaller period than for population abundances (approximately four generations) (Fig. 9d). Population and character evolution show discordant temporal fluctuations. Moreover, the potential for persistence rests on a kind of evolutionary dynamics that would be difficult to detect in data from natural populations.

Example 3: $\lambda^ = 11$*

A small increment in λ^* from the previous example suffices (due to the threshold nature of the 'control' in the system) to transform the system into one with episodic bouts of dramatic population instability (Fig. 9e and f). The refuge characters de-evolve gradually over an approximately 1000 generation period, associated with the refuge level going to zero (Fig. 9f). The absence of the refuge leads to large population fluctuations for approximately 100 generations (Fig. 9e), followed by the re-evolution of first the host character and then that of the parasitoid. The resulting low, but non-zero, refuge levels suffice to stabilize the system for another 1000 or so generations. Thus, the interplay of evolution and population dynamics can lead to episodic instability, punctuating periods of relative stability over long time scales.

Example 4: $\lambda^ = 12$*

A further increase in λ^* pushes the system to unambiguous BU control (Fig. 9g and h). Both populations (Fig. 9g) and their refuge characters (Fig. 9h) evolve and equilibrate to constant levels, with the parasitoid only moderately depressing the host.

It should be noted in the above examples that co-evolution has effects on ecological time scales, such as preventing population cycles and dampening oscillations that could lead to extinction.

Limits to character evolution

In the above analyses, both host and parasitoid characters were free to change – their tandem evolution could only be arrested by a joint marginal decrease in fitnesses at the equilibrium. We now consider how either keeping one character constant or limiting its maximum attainable level influences refuge evolution.

Constant characters

Figure 10 shows how holding mean character levels of either the host or the parasitoid constant may influence refuge evolution. This corresponds, for instance, to cases in which the additive genetic variance for one of the phenotypic characters is negligible.

Holding the host character \bar{n} constant at \bar{n}_c (Fig. 10a) impedes refuge evolution if $\bar{n}_c < \hat{n}$ (recall \hat{n} is the non-trivial equilibrium of the host character in the freely evolving system) simply because the parasitoid character is able to 'catch-up' to some extent with the (fixed) suboptimal character of the host. As \bar{n}_c approaches the local optimum \hat{n} , the parasitoid persists only if \bar{p}_0 and Γ_p are sufficiently large (not shown). If either of these quantities is too small the evolution of the anti-refuge character will be too slow to ensure parasitoid persistence (see also Gomulkiewicz and Holt, *in press*). If either is too large (e.g. $\bar{p}_0 \approx \bar{n}_c$), then the parasitoid will persist, but the refuge will be pinned at zero (as for sufficiently small \bar{n}_c ; not shown). As \bar{n}_c is still further increased, so too does the equilibrium refuge level increase, but to the detriment of host fitness. It is interesting that despite \bar{n}_c being suboptimal, a higher refuge ensues than when \bar{n} varies freely. Again, only if \bar{p}_0 and Γ_p are sufficiently large does the parasitoid invade and persist. Finally, there comes a level of \bar{n}_c beyond which the current intrinsic growth rate (λ_c) of the host itself approaches unity and, as a consequence, even if the parasitoid invades the system it does not persist long and may even lead to the associated extinction of the host (not shown).

When the parasitoid character \bar{p} is held constant at \bar{p}_c (i.e. $\Gamma_p \rightarrow 0$), but that of the host is allowed to vary, other interesting effects are observed (Fig. 10b). As long as $\bar{p}_c < \hat{p}$ the host evolves a smaller level of its own character, but a *larger* refuge than observed if \bar{p} varies freely. As

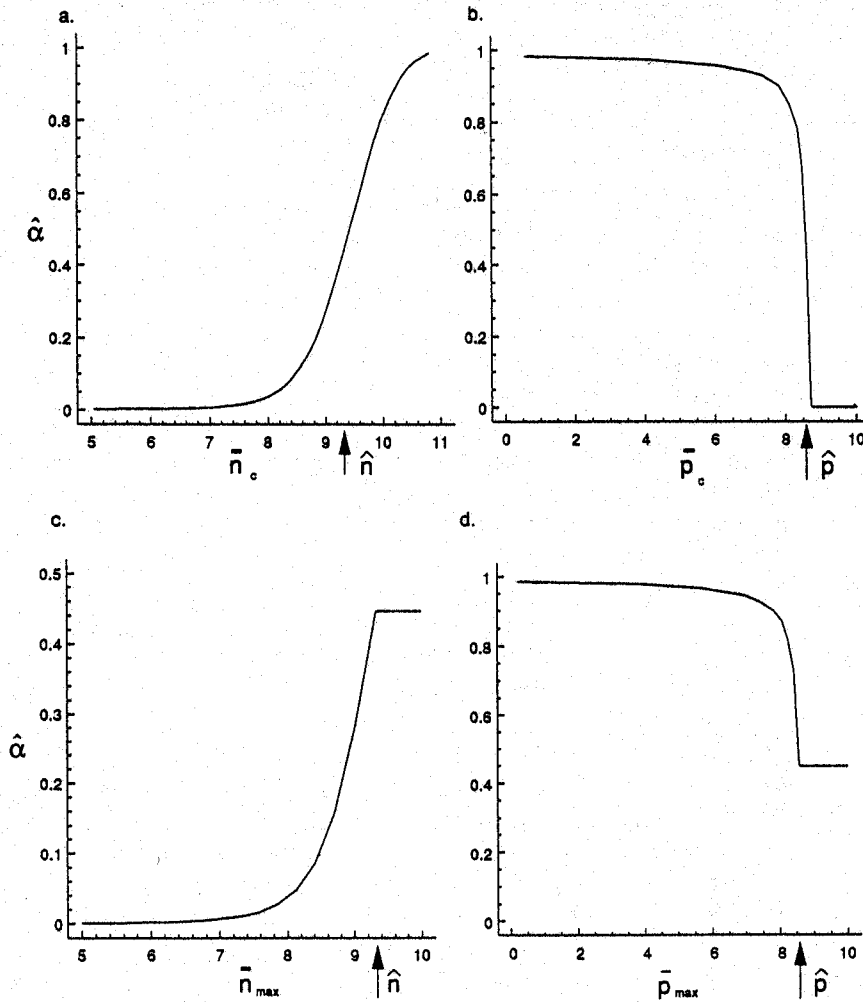


Figure 10. Influences of character constraints on the size of the equilibrium refuge. (a) Effect of constant levels of \bar{n} ($\bar{p}_0 = \bar{n}_c - 1$). (b) Effect of constant levels of \bar{p} ($\bar{n}_0 = \bar{p}_c$). (c) Effect of constraints on the maximum value of \bar{n} . (d) Effect of constraints on the maximum value of \bar{p} . Parameters otherwise as in Table 1, except $\lambda^* = 20$.

\bar{p}_c is pushed past \hat{p} , it becomes increasingly costly for the host to evolve a given level of refuge, reducing $\hat{\alpha}$. If \bar{p}_c is large enough, then R_0 drops below unity and the parasitoid does not invade. This scenario of a fixed parasitoid character may be relevant, for example, to fragmented systems where high \bar{p}_c is optimal in a source habitat, but not in a target sink system.

Upper limits to characters

Figure 10 also shows what happens when both characters can evolve but with constraints on the maximum attainable value (\bar{n}_{max} , \bar{p}_{max}) of one of them.

Free evolution of the parasitoid character can reduce the refuge up to a certain level of \bar{n}_{max} as long as $\bar{n}_{max} < \hat{n}$ (Fig. 10c). Interestingly, constraining the parasitoid character to be less than \hat{p} results in the evolution of a larger than normal refuge (Fig. 10d), suggesting a negative relation

between the *apparent* selection pressure of the parasitoid (i.e. \bar{p}_{\max}) and the level of the refuge evolved. Increasing \bar{p}_{\max} eventually erodes the refuge until, beyond $\bar{p}_{\max} = \hat{p}$ the evolved refuge remains constant at $\hat{\alpha}$.

Discussion

Similar to recent studies on consumer – resource co-evolution (e.g. Marrow and Cannings, 1993; Saloniemi, 1993; van Baalen and Sabelis, 1993; Frank, 1994), we found that ecology and evolution interact in complex and intriguing ways. In general, adding evolutionary dynamics to an unstable ecological model makes it more likely that the system will persist, simply because the absolute refuge can evolve. Although not considered in our model, we would predict that co-evolution could *destabilize* an otherwise stable ecological association if the host's refuge character existed at a stable state prior to the invasion of the parasitoid (e.g. as a consequence of co-evolution between the host and its food plant). An additional, striking finding of our study is that, at the threshold of refuge evolution, systems can enter quasi-stable regions, punctuated by periods of dramatic population dynamics and evolutionary change; sometimes this leads to extinction, and sometimes stability re-emerges. Assessing the generality of these conclusions should be an important task for future theoretical work.

Our results bear on a number of issues.

Conditions for top-down versus bottom-up control

The direction of population control in consumer – resource interactions is the key to theories of both population dynamics (e.g. Lawton and McNeill, 1979; Hochberg and Lawton, 1990) and community structure (e.g. Hairston *et al.*, 1960; Holt, 1977; Pimm, 1978; Tilman, 1982; Matson and Hunter, 1992; Hochberg and Hawkins, 1993; Holt and Lawton, 1993). In our model, a threshold effect demarcating the direction of control transpires when the host's carrying capacity (K) is sufficiently larger than its basic reproductive rate (λ).

There are four criteria which must all be satisfied for ecological TD regulation and an additional criterion which must hold for evolutionarily stable TD control.

(1) $\alpha\lambda < 1$. The ecological model predicts that the parasitoid will only have a severe impact on the host population if the latter cannot sustain a self-limited population in the refuge alone (Hochberg and Hawkins, 1993). There is evidence from biological control introductions that proportional refuges are indeed inversely linked to the potential of parasitoids to depress their hosts (Hawkins *et al.*, 1993).

(2) $R_0 \approx \eta > \lambda$. The ecological model says TD control requires that the maximum population growth rate of the parasitoid (\approx maximal attack rate) exceeds that of the host (e.g. Hassell, 1978; Hochberg and Lawton, 1990). Numerical simulations not presented here suggest that even though this particular criterion may not always apply, both η and λ are important in determining the direction of control when the parasitoid acts at other points in the host's life cycle (see also May *et al.*, 1981). There is currently insufficient data to assess this inequality, but it seems sensible that such data would be readily available for some systems once investigators are alerted to the importance of the comparison.

(3) Either $k < 1$ or both $k \approx 1$ and $\alpha > 0$. Given that condition (1) holds, then the stable TD control of the host population depends on sufficient, but not too high, levels of spatial heterogeneity in parasitism (e.g. Hassell, 1978, 1980; May, 1978). If $k < 1$, then no proportional refuge is necessary for the system to be locally stable, whereas for $k \approx 1$ small amounts of α are also necessary (Fig. 3b). Spatial heterogeneity levels consistent with the first of these criteria are

frequently found in nature (Hassell and Pacala, 1990). Figure 2 suggests that the second of these criteria is empirically observed as well.

(4) $K \gg \lambda$. The ability of the parasitoid to clearly dominate as a regulatory factor of the host obviously depends on the scope for such regulation, that is, on the host's carrying capacity and the minimum levels to which the parasitoid can regulate the host. This indicates that lower trophic level dynamics are important to how the third level (the parasitoid) influences the second (the host) (Hairston *et al.*, 1960). Carrying capacities satisfying this criterion are bound to be common in nature.

(5) $\eta^* C_p > \lambda^* C_n$. Whereas the above four criteria are based on ecological considerations, when refuge evolution is possible, achieving the first two criteria is tempered by the costs of refuge evolution. The additional criterion for TD control in evolutionary time contrasts both the maximal growth rates and the costs of the refuge characters across the two species. In the special case of equal costs to character evolution criterion (5) is equivalent to criterion (2). No data is currently available to assess this condition.

Our model predicts that in the absence of evolution, if any one of the first four conditions for TD control are contravened, either BU control will result (conditions 1 and 2) or the parasitoid (and possibly the host) will go extinct (condition 3), or the control will be intermediate between TD and BU (condition 4). Given evolution, negation of the fifth criterion alone will likewise lead to refuge evolution and BU control. The apparent stringency of this joint set of conditions is in accord with Hawkins' (1992) assertion that many, if not most, natural host-parasitoid systems should be characterized as having strong bottom-up effects.

In a more applied vein, our results have implications for biological control, where an exotic species of parasitoid is released to achieve the depression of the host population below an economic target (Hawkins *et al.*, 1993; R.D. Holt and M.E. Hochberg, in preparation). For instance, in screening potential biological control agents, it may be particularly useful to identify candidate parasitoids with relatively high values of η . This may seem obvious at first sight, but our study provides a fundamental eco-evolutionary basis for this criterion. Moreover, it seems likely that pest species often will be characterized by large λ (permitting high, equilibrium abundances and dramatic outbreaks). Our theoretical results suggest that these species, unfortunately, might be just those that are able to overcome effective limitation by biological control agents, via their evolutionary responses. Evolutionarily stable biological control requires hosts that cannot evolve effective refuges (e.g. because they are too costly).

Often species will show spatial variation in their basic demographic parameters. For instance, a host may have a lower λ at the edge of its range than in its centre. Our models suggest that host species might be expected to be less regulated by parasitoids (to values well below K) near the centre of their ranges, because of co-evolutionary responses. This is opposite to what would be expected, with host parameters fixed.

Demographic extinction of invaders

One of our major predictions concerns the invasibility and persistence of a parasitoid dependent on the size of the host population. Gomulkiewicz and Holt (in press) have recently shown that when small numbers of colonists arrive in a new habitat to which they must adapt, population persistence depends on a sufficient capacity for and speed of evolutionary change, so as to avoid extinction via the effects of demographic stochasticity. Our results extend theirs by showing that an invading parasitoid can go demographically extinct if its anti-refuge character does not evolve sufficiently fast (Figs 10a and b), relative to the evolutionary response of the host. Both the initial ecological and evolutionary conditions in the system can thus determine the chances for species persistence in a novel environment.

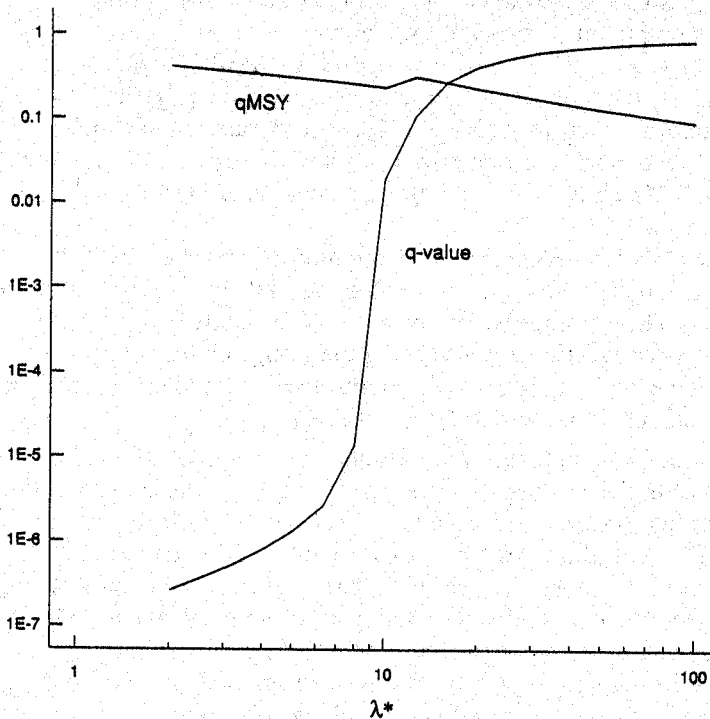


Figure 11. Comparison between equilibrium q -values generated by the co-evolutionary model and those predicted (Hassell and May, 1985) to permit exploitation of the host population at the maximum sustainable yield. The blip on the q -MSY line corresponds to the switch from systems with no evolved refuge (i.e. $\lambda^* \leq 10$) to those evolving a refuge. The q -MSY curve, based on the cost-free intrinsic growth rate of the host (λ^*) is virtually the same as that shown in the figure (based on $\hat{\lambda}$).

Are parasitoids prudent?

Slobodkin (1972, 1974) argued that when prey populations evolve defences to their predators, the evolutionary outcome may be that the predators appear 'prudent'. Slobodkin (1972, 1974) further argued that evolutionary dynamics in predators leading towards maximizing a sustainable yield for the exploitation of prey is problematic, since it almost unavoidably involves group selection. Prompted by his arguments, Hassell and May (1985) used an ecological model to evaluate the 'prudent predator' hypothesis. They argued that in certain cases of biological control (Beddington *et al.*, 1978), parasitoids depressed their host populations well below the theoretical maximum sustainable yield (MSY).

Our co-evolutionary model can be used to investigate whether or not evolution takes the system to or very near the MSY. Figure 11 compares the effects of the cost-free, intrinsic growth rate of the host (λ^*) on the q -value of the MSY ($q_{MSY} = 1/(1 + \sqrt{\lambda})$; see Hassell and May, 1985) and the equilibrium q -value after evolution ($q = \hat{N}/K$). As long as the refuge does not evolve (i.e. $\lambda^* \leq 10$ in Fig. 11) the parasitoid depresses the host well below the level leading to the MSY, whereas evolution of the refuge is accompanied by exploitation of the host at a level somewhat above the abundance giving MSY (Fig. 11). (Note that this could be interpreted as 'apparent prudent predation' (Slobodkin, 1972).) Thus, in agreement with Slobodkin's arguments (1972, 1974), we find that evolution does not give rise to natural enemies (parasitoids)

which exploit their prey (hosts) at or very close to the MSY. Exploitation levels depend on which species evolutionarily dominates the association. Our model suggests that this will often be the host species.

Some testable predictions

The theory developed here can be used to formulate a number of testable predictions. Assuming the systems investigated are at an evolutionary equilibrium with respect to the refuge, the presence of absolute refuges should be associated with (1) hosts having large populations in the absence of the parasitoid (i.e. high K), (2) hosts living in relatively homogeneous environments (i.e. high k), (3) hosts having large basic reproductive rates compared with their parasitoids (i.e. $\lambda > \eta$), (4) parasitoids with very low basic reproductive rates (i.e. $\eta \rightarrow 1$) and (5) a self-sustaining subpopulation of the host (i.e. $\alpha\lambda > 1$).

These factors also tend toward systems in which the host is largely regulated by its own density dependence, with substantial bottom-up control (namely, $0.1 \leq q < 1$).

Testing the predictions

Testing the predictions of our theory will require a blend of comparative and experimental studies. We foresee this to be a daunting task. Here we briefly outline some issues associated with estimation methods.

(1) **Cost-free, intrinsic growth rates.** λ^* and η^* correspond to the potential population growth rates of host and parasitoid, respectively, in the absence of their *evolved* refuge characters. If the maintenance of the character is due to the selection pressures involved in the host-parasitoid association, then proxy estimates can be made from the intercept of the regression of reproductive value (in the absence of competition) versus character size. Although not modelled in our system, if the character already existed at an evolutionary stable state prior to parasitoid invasion (and was prone to subsequent amplification through co-evolution), then λ^* and η^* should be estimated prior to the establishment of the parasitoid using, for example, lifetable techniques (Manly, 1990).

(2) **Character costs.** Estimating character costs, C_n and C_p , is apt to be quite challenging. An approximate method may be to regress the loss in the reproductive values of the host (i.e. $\lambda^* - \lambda_t$) and parasitoid ($\eta^* - \eta_t$) with a reliable index of the evolved characters (i.e. \bar{n}_t and \bar{p}_t , respectively). In some cases, such as parasitoid ovipositor length versus host depth within a twig, estimates of the index may be relatively straightforward.

(3) **The proportional refuge.** The proportional refuge, α , is the minimum rate of host survival from the parasitoid, independent of parasitoid density (Hochberg and Hawkins, 1994) (Fig. 1). Examples of studies estimating the level of such refuges already exist (Hawkins *et al.*, 1987; Murdoch *et al.*, 1989). Assuming that host density has no effect on its asymptotic survival rate from parasitism (see Fig. 1), the proportional refuge can be estimated from the asymptotic regression of host survival from parasitism (Y) on parasitoid density (X), that is $Y = 1 - C_1(1 - \exp\{-C_2X\})$, where the refuge α is given by $1 - C_1$. In many cases, special methods are required to measure percent survival from parasitism accurately (van Driesche *et al.*, 1993).

(4) **Probabilistic refuges.** Hassell and Pacala (1990) have developed methods for estimating the level of spatial heterogeneity in a system. Methods for estimating k , as employed in our model, will have to separate the total refuge into its probabilistic and absolute components (see Fig. 1; Perry and Taylor, 1986).

A note about probabilistic refuges and some future directions

We have employed a phenomenological approach to modelling refuge evolution, whereby only the absolute component of all possible refuges is permitted to evolve (i.e. k stays constant). One could argue that increasing the proportional refuge may be positively associated with increases in probabilistic refuges, because greater deviations between the mean host and parasitoid phenotypes will increase the non-concordance between relative host and parasitoid densities at any point along a phenotypic character axis. This non-concordance makes hosts with the highest character states (but *are not* in the proportional refuge) less vulnerable to parasitoid attack than those with smaller character states. Although we did not include this property in the model, we expect our general conclusions about total refuge evolution to still hold (i.e. some combination of absolute and probabilistic components), albeit with smaller expected levels of α and more pronounced probabilistic refuges (embodied in the parameter k of our model).

Further modelling studies need to be conducted to either confirm or refute our basic findings. Such models could include (1) forms of host self-limitation other than 'contest' competition, (2) orderings of density-dependent mortalities in the host's life-cycle other than the one considered here, (3) more complex cost functions, (4) an explicit consideration of variation in the risk of parasitism rather than a phenomenological refuge function and (5) explicit population genetics. A particularly important task will be to canvass case studies from biological control, to determine the utility of our results for interpreting cases of the breakdown of control.

Acknowledgements

We wish to thank B.A. Hawkins for kindly providing the frequency data presented in Fig. 2. We are grateful to R. Gomulkiewicz, Y. Michalakis and M. Slatkin for helpful discussions and to M. Rosenzweig and L. Slobodkin for comments on the manuscript. This work was funded by the French Ministry of the Environment (program EGPN), the University of Kansas and the National Science Foundation. RDH wishes to thank, in particular, R. Barbault, J. Clobert and their associates and staff for their hospitality during his visits to Paris. We thank our wives for their continued tolerance.

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