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A tantalizing application of our model is to the biological control of insect pests. This study together with previous ones (e.g. Beddington *et al.* 1978; Hassell 1978; May and Hassell 1981, 1988; Hochberg and Hawkins 1993) make both general and specific predictions about the desirable attributes of a parasitoid for use in biological control programmes. An important challenge for the future is to test these predictions, enabling us to evaluate the validity of the underlying population dynamics theory.

Summary

Explaining the genesis and maintenance of insect parasitoid richness is fundamental to understanding larger patterns of biodiversity. Recent applications of population dynamics theory to the maintenance of species richness has yielded a number of insights into why some parasitoid assemblages are speciose and others are species poor. One of the major determinants of species richness predicted by these models is the presence of 'refuges', such that a proportion of the host population is always invulnerable to parasitism. The predictions of these models are in partial accord with empirical studies comparing refuges based on host feeding niche alone.

In this chapter we employ a very simple model to illustrate how proportional refuges to parasitism can be expected to influence parasitoid species richness. We then compare the predictions of this model to more realistic formulations; the concordance between the patterns generated by the two modelling approaches vouches for the robustness of proportional refuges as theoretical determinants of richness. We re-examine the data on parasitoid richness by estimating the total refuge using maximum parasitism rates. The refuge-based patterns generated by the simple model are in general accord with the data set, although a substantial amount of variation in the data remains unexplained by maximum parasitism rates.

If our model is correctly reflecting the influence of species interactions on parasitoid richness then it should be usable as a predictive tool. We explore several theoretical and empirical applications of our theory. First, we explore the accord between current biological hypotheses and predictions of the model with regard to explaining why tropical parasitoid assemblages have low species richnesses as compared with temperate systems. Second, we describe some of the evolutionary pressures that may have moulded current patterns in parasitoid richness. Third, we outline conditions for which interactions between the herbivore and parasitoid trophic levels are controlled from the top-down or from the bottom-up. Fourth, we link our theory to the release of one or more species of parasitoid for the control of an insect pest, presenting a quantitative criterion to explain the most spectacular biological control successes. Finally, we briefly outline how refuges can be estimated using field experiments.

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Hawkins and Gross (1992) found that the most species-rich systems are those most likely to result in biological control success, but they used only holometabolous host systems in their analysis. It is possible that had they included Homoptera, the positive relationship they found between species richness and biocontrol success would have been obscured. This is supported by the findings that: (a) Homoptera on average have fewer parasitoid species than holometabolous species (Hawkins and Lawton 1987); and (b) Homoptera represent the taxonomic group with the highest rate of biocontrol success (Hall *et al.* 1980). The example provided by Rose and Debach (1992) illustrates how at least some Homoptera may occupy minimal refuges and, as a consequence, are under strong biological control. Therefore, our model's predictions are consistent with empirical findings.

Refuges and the selection of a biological control agent

What does our model tell us about the attributes of a parasitoid that make it a good control agent?

In accord with previous studies (e.g. Beddington *et al.* 1978; Hassell 1978; Hochberg and Hawkins 1992, 1993), we predict that, once a parasitoid is introduced into a host population, long-term control is increasingly likely to occur as $\lambda \rightarrow 1$. We argue that this is because at low basic reproductive rates:

- (1) even hosts with large refuges are controllable;
- (2) the host population is slow to generate resistant genotypes; and
- (3) the costs associated with evolution of a refuge are apt to be high compared with their associated decreases in the risk of being parasitized.

It should be pointed out that in real systems 'breaking' the host's refuge (i.e. $\alpha\lambda < 1$) may simply mean that the parasitoid is able to launch attacks at points in the host's life-cycle when the latter is most vulnerable to parasitism. Our model indicates that the selection of either these 'refuge-avoiding' parasitoids or the previously mentioned 'refuge-breaking' parasitoids is of primary importance for the achievement of striking success in biological control programmes.

The question of how the degree of polyphagy of the introduced parasitoid will influence its success as a biological control agent has attracted much attention (see Waage 1990). The main argument for host specificity is that attacks are concentrated on the target pest, leaving the populations of non-target insects unaffected. Models including host refuges to parasitoid attack show that some degree of parasitoid polyphagy is actually *desirable* as long as $\alpha\lambda < 1$ for the target host and $\alpha'\lambda' > 1$ for non-target hosts (Hochberg and Hawkins 1993). Under such circumstances non-target hosts (if abundant and not the object of species conservation) are far less affected by the parasitoid than are target hosts. These non-target hosts act as an important 'reservoir' for the parasitoid, providing a sort of inundative input into the parasitoid population attacking the target host.

Finally, we argue that a quantitative criterion based on proportional refuges and the host's basic reproductive rate needs to be met to attain the most striking successes in classical biological control (*sensu* Beddington *et al.* 1978). This is not to say that control is not possible if this criterion is not met (Table 23.1); 'success' depends on the achievement of a control objective (Waage 1990).

If our aim is to reduce the host population to minimum mean densities, a criterion permitting this, developed in the context of parasitoid species richness (Hochberg and Hawkins 1992, 1993, and this study), is that the total refuge of the host to parasitism is sufficiently small, or

$$\alpha < 1/\lambda \quad (7)$$

Intuitively, this criterion means that the reproductive rate of 'refuge hosts' ($\alpha\lambda$) is insufficient to generate a self-regulated sub-population of the host. In the context of the simplified model presented here, this criterion is $\alpha < (1/\lambda - f_0)/(1 - f_0)$.

Measuring refuges

Our model uses the extent of a host's refuge as a predictor of the species richness of parasitoid communities. Estimating the contributions of proportional and probabilistic refuges to explaining variation in host susceptibility to parasitoid attack is likely to be problematic for many systems. When possible, it is essential that the host's refuge be estimated from at least several data points (i.e. host generations and/or host patches within a given generation). It is also important that the spatial sampling scale reflects the population-level variability in susceptibility to parasitoid attack. The total proportional refuge, independent of host and parasitoid densities, is estimated as the intercept in the regression of generational host survival from parasitism as a function of host density and adult female parasitoid densities. Furthermore, the host refuge with respect to a given species of parasitoid can be estimated using replicated experiments exposing laboratory or caged field populations of the host to various densities (i.e. treatment) of a single parasitoid species (see e.g. Hawkins *et al.* 1987).

Conclusions

Our main purpose has been to see if empirical species richness patterns can be explained by population dynamics theory. It can. Nevertheless, according to the model and the data refuges alone cannot explain all of the variation in species richness; our model shows, in an unconvoluted way, how other demographic processes can account for much of the residual variation. Further, the fact remains that despite any concordance between model predictions and data the theory has yet to be fully tested. As a first step in the context of our models, this will require the estimation of key parameters for real parasitoid complexes.

Evolutionary pressures and refuge-breakers

Our model does not consider how the host and its parasitoids may evolve through time. Evolution in the context of species diversity is important because it provides a mechanism for the generation of diversity in the first place. Our theory provides an ecological explanation for the maintenance and loss of this diversity over relatively short periods of time.

The rate of refuge evolution should depend, in part, on the host's basic reproductive rate. All else being equal, hosts with high values of λ should evolve refuges rapidly, both because of the rapid generation of resistant individuals and the substantially lower risk of parasitism associated with small increases in the quantitative refuge characters. It is tempting to conjecture that natural systems should conserve species richness, driven by host-parasitoid coevolution to intermediate levels of refuge. The theoretical case of 'refuge-breakers' (see below) is an argument against this. A pressing necessity in future empirical work is to know the frequency in natural systems where a parasitoid limits or regulates its host to very low equilibrium levels, associated here with low refuge levels and low species richness.

Parasitoids must evolve specializations if they are to exploit the better protected hosts. Host species with potentially difficult refuges to exploit (e.g. wood borers and root feeders) should be attacked by parasitoids with behavioural and/or morphological specializations, whereas leaf miners, for instance, should be exploited by species with less sophisticated adaptations for penetrating host tissues. We also expect the diversity of a host species assemblage itself to be pivotal in determining the patterns of polyphagy in parasitoid assemblages (MacArthur 1972). Species-rich host assemblages with little heterogeneity in refuge types can be expected to be exploited by species-rich, polyphagous parasitoid assemblages (see also Godfray 1994; Askew Chapter 10). As refuge heterogeneity increases, parasitoids should become increasingly monophagous, and, as predicted by Hochberg and Hawkins (1992), species richness should decrease.

Our model assumes that the host refuge affects all parasitoid species equally. This is bound to be an oversimplification of reality, and even more so given the fact that a multitude of refuge generating mechanisms may be at the disposal of the host. According to our theory, for a host individual to be 'in the refuge' it needs to be protected by one or more refuge-generating mechanisms over the full period of attack of the parasitoids. Nevertheless, only a single species of parasitoid need be able to 'break' the total refuge of the host (i.e. $\alpha\lambda < 1$ for parasitoid species i) for the richness of a given assemblage to change substantially (Hochberg and Hawkins 1993). How substantial a drop in richness will depend on the exploitation potential of the parasitoid. Likewise, evolution of resistance on the part of the host against the same 'refuge-breaking' parasitoid can result in a large gain in species richness, either from the invasion of parasitoids from other populations and/or the increase in density of previously rare parasitoid species.

Host population regulation

The extent that natural enemies act as regulators of prey populations is debatable (e.g. Lawton and McNeill 1979; Hochberg and Lawton 1990; Hawkins 1992), the best evidence coming from managed systems, and systems involving non-native natural enemy or herbivore species (Crawley 1992b). The related question of whether host-parasitoid coevolution can result in the exploitation of the host at or near the maximum sustainable yield (meaning that the parasitoid is not a strong regulator of the host) is an interesting one and deserves further attention (Hassell and May 1985). Our richness data, as it stands, cannot be used to quantify the frequency of 'top-down' control of hosts in natural systems. (We use the term 'top-down' to mean the propensity of variation in the parasitoid population to explain spatial and temporal patterns of the host population.) Although the general richness pattern is apparently inconsistent with patterns produced by strong top-down systems (i.e. low species richness at low levels of refuge), species depauperate cases do exist, and even when systems are species rich, we do not know the extent to which the parasitoids are influencing host numbers. What is urgently needed are experimental investigations of natural systems.

It is appealing that processes identified as being pivotal in simple consumer-resource and competitive systems should be the same ones generating richness patterns in multispecies systems (see Table 23.1). Consumer-resource interactions determine the general richness pattern across host species, as a result of the impact of the parasitoids on host (i.e. resource) density. Competitive relationships between the parasitoid species are important in determining the particular parasitoids represented in the richness measure. It is worth reiterating that if we do not know the basic reproductive rate of the host within the refuge ($\alpha\lambda$) and the exploitation rates (f_i 's) and competitive relationships (n) of the parasitoids, then parasitoid species richness cannot alone identify systems under strong top-down and bottom-up control (see below).

Biological control and species richness

Our model predicts that parasitoid species richness prior to an introduction is not necessarily a good indicator of the controllability of the host; rather, we suggest that hosts with the smallest refuges with respect to the introduced parasitoid should be the best controlled (Table 23.1). (By 'control' we mean the persistent reduction of the pest population to low densities, based on economic targets.) Once the parasitoid species is introduced for control of the host, we predict that the best controlled systems should settle to relatively low levels of parasitoid species richness, although species-rich systems can be associated with a host population depressed below the economic threshold, but not too low for local extinction of competitively inferior parasitoid species to occur.

Chapter 15). Hawkins (1990) found that a relative paucity of parasitoids in the tropics also exists in individual parasitoid complexes, as would be expected based on regional species richness relationships between parasitoids and hosts (fewer or equal numbers of parasitoid species diffused over many more host species). Most of the losses in parasitoid species richness were found among exophytic hosts.

What can the model tell us about potential mechanisms that might account for latitudinal gradients in parasitoid community richness? To explore this, hosts were classified by mean low temperature for the coldest month in the habitats in which they were studied (Hawkins 1990). Two classes were distinguished: mean low temperature more than 10°C (tropics and sub-tropics) and mean low temperature less than 10°C. The geometric mean of temperate parasitoid species richness is significantly greater than that for the tropics (mean $\pm$ 1 SE, temperate = 4.71 ± 0.19 versus tropics = 3.69 ± 0.19 , ANOVA: $F=12.65$, $p<0.001$). When hosts are ranked in terms of percentage parasitism, both groups show monotonically decreasing levels of parasitoid richness (Fig. 23.6). The main difference between the climatic zones is that for those studies in which parasitism is low to intermediate, temperate parasitoid communities are richer than tropical ones (Fig. 23.6; see also Hawkins 1990).

Based on our models, we distinguish three forces which may contribute to explaining the relative paucity of parasitoid species in the tropics as compared with temperate zones:

1. *Interspecific competition.* For higher levels of interspecific competition to occur, the model predicts that tropical systems should be characterized by: (a) relatively high basic reproductive rates of the parasitoids; and/or (b) relatively low basic reproductive rate and carrying capacity of the host population; and/or (c) little niche separation for parasitoid assemblages dominated by species having restricted host ranges. Note that none of the biological hypotheses make explicit reference to interspecific competition.
2. *Predation.* The model predicts that tropical parasitoids should have relatively low basic reproductive rates due to generalist predators and hyperparasitoids. The host predation and adult parasitoid predation hypotheses both suggest this as a mechanism limiting tropical parasitoid richness.
3. *Population growth.* The model predicts that tropical hosts should have: (a) relatively high refuge levels (i.e. high α); and/or (b) that tropical parasitoids should have low basic reproductive rates independent of generalist predators. The former condition is suggested by the nasty host hypothesis and the latter by the resource fragmentation hypothesis. There is no statistical difference between maximum parasitism rates in tropical and temperate systems (mean rates, corrected for differences in species richness: 35.1% in tropics and 39.4% in temperate zone, ANOVA: $F=3.27$, $p=0.071$), thus not in clear support of the expectation based on the nasty host hypothesis that hosts in the tropics are relatively protected from their parasitoids.

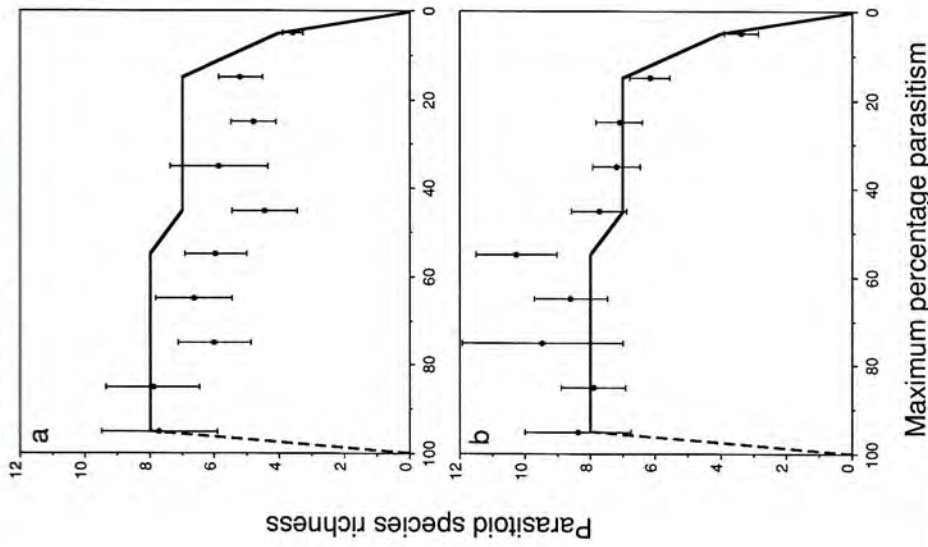


Fig. 23.6 Comparison of model fit to full data set (Fig. 23.5) with mean ($\pm$ 1 SE) parasitoid species richness for (a) hosts inhabiting areas with a mean low temperature $>10^\circ\text{C}$ in the coldest month (tropics and sub-tropics) and (b) hosts in areas with a mean low temperature $<10^\circ\text{C}$ (temperate zones).

Clearly, without more supporting data the model cannot conclusively assess the relative contributions of the four biological hypotheses to explaining lower species richness in tropical systems. On the other hand, it is encouraging that differences in tropical versus temperate parasitoid species richnesses can be accounted for in the model by examining the effects on model parameters of mechanisms suggested by empirical study, and the model identifies which parameters should be measured if we are to be able to distinguish underlying mechanisms. The model provides a robust theoretical tool for exploring the constraints of parasitoid species richness generated by simple population processes.

parasitism data extracted from the extensive primary literature on herbivorous insects, ranked by host feeding niche. We argued that, *all else being equal*, structural refuges to parasitism provided by the host's food plant were sufficient to explain the general species richness pattern for endophytic hosts, but failed to explain the full pattern when exophytes are included, because exophytes generally support either too many or too few species. We suggested that this reflected that many exophytic herbivores, which occupy small or negligible structural refuges, derive protection from parasitoid attack by refuges provided by other defences, such as behaviours or chemicals.

Recognizing that refuges may have several sources permits an alternative approach for comparing the model with real parasitoid complexes. The maximum parasitism rate achieved by parasitoids on a host provides a measure of the host's innate susceptibility to attack, irrespective of the nature of its refuge; a herbivore which can suffer up to 100% parasitism clearly occupies a minimal total refuge, whereas a host which is never parasitized more than say, 5% probably occupies an extensive refuge.

To examine parasitoid species patterns incorporating the full range of potential host refuges, whether structural or otherwise, we classified 819 species of holometabolous herbivorous insects for which parasitism rate data are available (Hochberg and Hawkins 1992; Hawkins 1993b) into 10 parasitism rate classes, with mid-points ranging from 5 to 95% parasitism. The overall pattern of the data (Fig. 23.5) is monotonically decreasing within the range of mid-points. The general shape of the richness-parasitism relation-

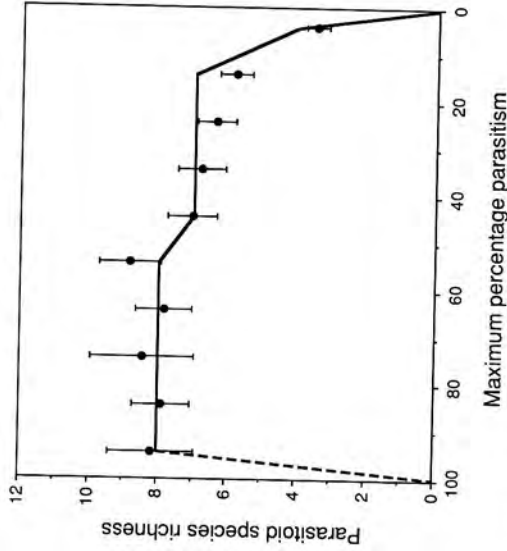


Fig. 23.5 Relationship between mean (± 1 SE) parasitoid species richness (the number of parasitoid species per host species) and maximum reported parasitism rate for 819 holometabolous host species, classed into 10, 10% parasitism levels (see Hawkins 1993a). The solid line shows one possible 'fit' of the data by the model; parameter values: $x=8$, $n=1.9$, $Q=150$, and $\lambda=20$.

ship broadly follows that which can be generated by the model (Fig. 23.5). The concordance is not perfect, but given the large errors apt to be incurred in estimating maximum percentage parasitism (e.g. Van Driesche *et al.* 1991), it is encouraging that the model can actually fit the data quite well.

It is clear from the error bars in Fig. 23.5 that refuges alone do not explain all of the variation in species richness. Much of this variation undoubtedly arises from the highly variable quality of the parasitism data. But, based on the model, we suggest that any real variability not due to measurement error results to some extent from study differences in: (a) host basic reproductive rates; and/or (b) parasitoid exploitation rates of their host population. Their effects on richness are accounted for by our model.

The dotted line in Fig. 23.5 corresponds to theoretical cases in which the host refuge is so low that host density is reduced to the point where many parasitoids cannot persist, or at least occur at densities too low to be sampled. It appears that in our sample of holometabolous hosts few, if any, occupy low refuges. Among the Homoptera, on the other hand, such cases may exist. For example, Rose and DeBach (1992) reported that while searching for parasitoids of the bayberry whitefly (*Parabemisia myricae* Kuwana) in its native Japan, herbivore populations were always low, and yet were heavily parasitized. In many areas they were able to find only dead whiteflies, and hence could recover no parasitoids. Ultimately, after intensive sampling over many host populations, five parasitoid species were reared. Three species were imported to California, where the whitefly was a serious pest, and were easily established. Subsequently, a species native to California was discovered attacking the whitefly at high rates in a few host populations. When this parasitoid was distributed into whitefly populations in which the introduced parasitoids had been established, host mortality rates rapidly approached 100%, and the Japanese parasitoids were no longer recovered. Complete biological control of the whitefly was accomplished in about 4 years. Clearly, when hosts occupy no refuge, and parasitoid attack rates are high, competitively superior parasitoids can reduce species richness to minimal levels through the exclusion of competitively inferior parasitoid species. Such cases are in full accord with the predictions of the model.

Temperate versus tropical species richness

How useful is the model for examining more detailed questions concerning constraints on parasitoid species richness? An important unresolved issue in parasitoid ecology is why at least some parasitoid groups do not appear to be richer in the tropics than in the temperate zones (Owen and Owen 1974; Janzen and Pond 1975; Janzen 1981; Gauld 1986; Askew 1990). A number of biological hypotheses have been proposed to account for this, which include: resource fragmentation (Janzen and Pond 1975); predation of parasitized hosts (Ratheke and Price 1976); predation of adult parasitoids (Gauld 1987); and host food plant allelochemicals (Gauld *et al.* 1992; Gauld and Gaston

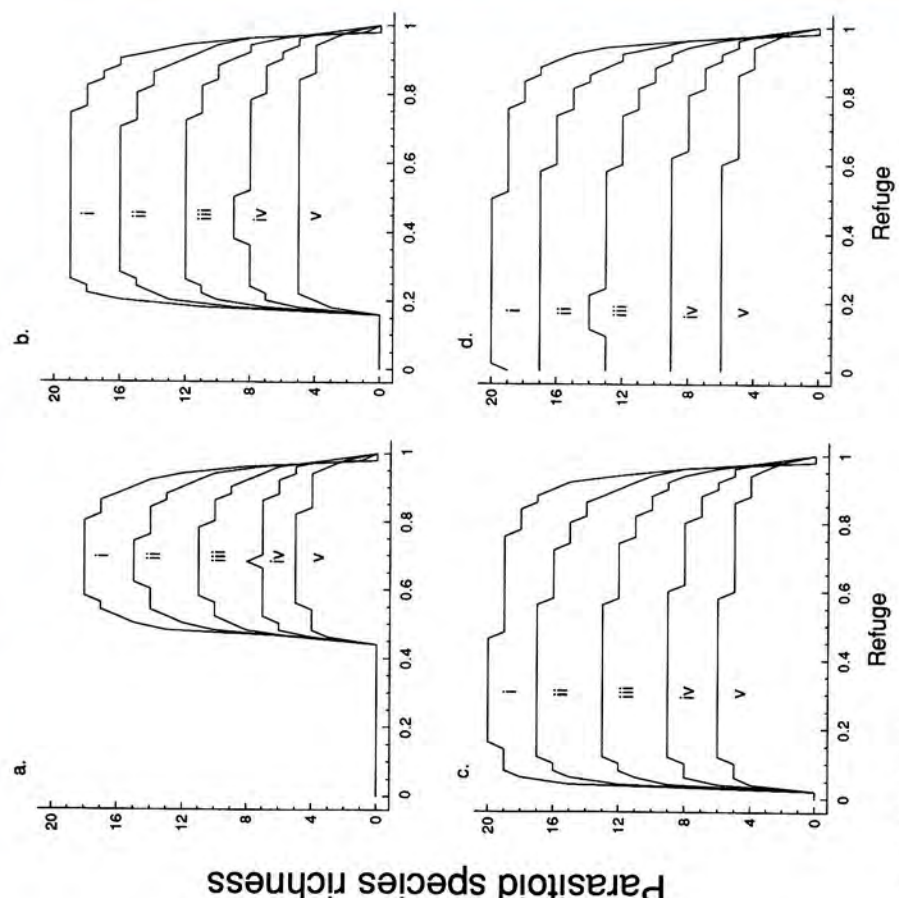


Fig. 23.3 Species richness for assemblages of 20 species of parasitoid. Curves (i) $n=1$, (ii) $n=2$, (iii) $n=4$, (iv) $n=8$, (v) $n=16$. Veil line is set at one surviving parasitoid individual at equilibrium, with $Q=200$, $\beta=2.3$, corresponding to a total survival rate from parasitism of 0.1. (a-d) as for Fig. 23.2.

population and other species ('generalists') are less influenced by the host. Hochberg and Hawkins (1992, 1993) have recently considered how proportional refuges act to determine richness patterns of multispecies parasitoid assemblages. Their models produce two basic patterns:

1. Dome-shaped. Hosts which have a sufficiently small refuge may be driven to virtual extinction or to densities too low to sample in a given locality. Parasitoid richness is either not counted (host is too rare to sample) or counted as being zero (parasitoids are too rare to sample, or extinct). The main difference in the shapes of generalist and specialist assemblages in relation to the host refuge is the more abrupt approach to maximum richnesses for the latter.

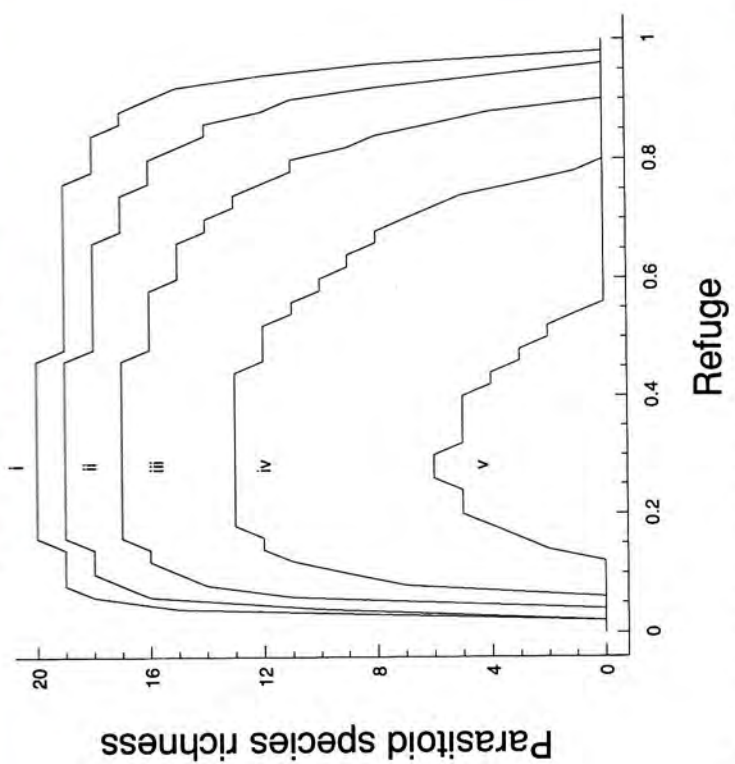


Fig. 23.4 Effect of veil line on richness. Minimum number of parasitoids required to be counted in the richness measure: (i) 1, (ii) 2, (iii) 4, (iv) 8, (v) 16. Other parameters: $\lambda = 8$, $n=1$, $Q=200$.

2. Monotonically decreasing. This can arise either if small-refuge hosts are: (a) not regulated by the parasitoids, or (b) regulated as for the dome-shaped pattern, but the sample is taken over a large enough geographical area to obtain an accurate sample of the host and parasitoid populations.

In addition to these fundamental patterns, as would be intuitively expected, rich generalist assemblages are more easily generated than rich specialist ones, the latter requiring either low levels of direct competitive interactions or an inverse relationship between interference and exploitative competition (Hochberg and Hawkins 1993).

Despite the crudeness of the model presented in equations 1 and 2, the patterns it produces, and the reasons for why they occur, are in accord with more realistic models, attesting to the robustness of some of the hypothesized determinants of species richness.

Empirical data on refuges

Hochberg and Hawkins (1992, 1993) presented species richness and percentage

abruptly, approaching Q when all of the hosts are in the refuge. If λ and/or f_1 are adequately large, then the pattern is simply a monotonic increase towards Q .

The patterns of parasitoid density are different (Fig. 23.2). In general, as λ and/or f_1 increase, parasitoid density increases and its maximum is shifted to lower levels of α . Trivially, for refuge levels where the host is extinct, so is the parasitoid. Thereafter, parasitoid density increases, attaining a maximum at intermediate levels of refuge, subsequently decreasing towards zero (attained at $\alpha = 1$). If λ and/or f_1 are sufficiently large, then parasitoid density decreases monotonically over all α (e.g. cases iv and v, Fig. 23.2d).

The mechanisms acting here are very simple. A combination of high exploitation rate of the parasitoid and little refuge for the host population are responsible for the host going extinct for $\alpha < (1/\lambda - f_1)/(1 - f_1)$. But as parasitoid exploitation decreases and/or the refuge increases beyond the point $\alpha = (1/\lambda - f_1)/(1 - f_1)$, the host produces what amounts to a self-sustaining sub-population. As long as the exploitation rate of the parasitoid remains constant from generation to generation, host and parasitoid numbers are positive. Beyond the point $\alpha = 1/\lambda$, no matter what the exploitation rate of the parasitoid, the host persists. The number of parasitoids produced increases with refuge strength until a point at which hosts potentially available for parasitism increase at a slower rate than does the number of these hosts that are invulnerable to parasitism. The result is that parasitoid numbers eventually drop to zero. The overall pattern of parasitoid abundance versus host refuge is dome-shaped if exploitation rate, $1 - f_1$, is sufficiently high (and/or λ sufficiently low), becoming monotonic decreasing for sufficiently small $1 - f_1$ (Fig. 23.2).

Multi-parasitoid assemblages

It is apparent from the structure of the population model that if we were to add other parasitoid species to the system, total parasitoid abundance would assume the same general patterns produced in Figure 23.2. In more general models (see below), the relative abundances of more than one parasitoid species are determined by (a) their intra-host competitive relationships; and (b) the distribution of exploitation terms (the f_i 's). Below the second determinant is considered for our simple model.

The survival rate, f_i , of hosts from species i , from an assemblage of x species is assumed to take the form

$$f_i = \exp \left\{ -\beta i^n / \sum_{q=1}^x q^n \right\} \quad (6)$$

where the survival of the host from the full parasitoid assemblage is $f_c = \exp\{-\beta\}$ and exploitative competition becomes increasingly equitable from species to species as $n \rightarrow 0$.

Table 23.1 Effect of total host refuge levels on various indices^a

	$\alpha\lambda < 1$	$\alpha\lambda \approx 1$	$\alpha\lambda \geq 1$
Species richness ^b	Low	High	Low
Host abundance	Low	Medium/high	High
Potential effectiveness of biological control	High	Medium/low	Low
Species interactions	Top-down ^c	Bottom-up	Bottom-up

^a Indices assume parasitoid(s) with high attack rates.

^b Measured as the propensity to sample parasitoid species per unit area.

^c Top-down control is not inevitable for $\alpha\lambda < 1$, as identified in more detailed models (Hochberg and Hawkins 1992, 1993).

After solving equation 5 for each parasitoid species, we counted each of them as contributing to richness if it exceeded an arbitrary density (the 'veil line' of Preston 1962) after accounting for density-dependent mortalities. Table 23.1 summarizes how different total refuge levels influence the system.

Similar to the parasitoid abundance curves (Fig. 23.2), the richness pattern is dome-shaped (Fig. 23.3), although the details of the richness and abundance shapes differ. This is due to the sampling threshold used in the richness measure. Generally, richness increases abruptly from zero to maximum at $\alpha = (1/\lambda - f_c)/(1 - f_c)$, followed by a plateau at intermediate levels of α , and a more or less gradual decrease to zero species richness as the risk of parasitism decreases (Fig. 23.3).

Again, as for the case of a single parasitoid, for large values of λ (Fig. 23.3d) and f_c (not shown):

- (1) the dome-shape gives way to a monotonically decreasing form;
- (2) the magnitude increases over a range of α ; and
- (3) the peak shifts to lower α .

As the distribution of exploitation among the parasitoids becomes increasingly disparate (i.e. n increases), fewer species contribute to the richness measure (Fig. 23.3). This is simply because the competitively inferior species become increasingly rare with increases in n (i.e. decreases in their exploitative competitiveness). Finally, as expected, the veil line plays an important role in perceived richness (Fig. 23.4). Increasing the line decreases richness, with most of the loss in richness information occurring at low and high levels of refuge.

Patterns produced by more realistic models

A more general and realistic model than that in equations 1 and 2 should include a per capita risk function of parasitoid attack (e.g. Hassell 1978), in which some parasitoid species ('specialists') are tightly coupled to the host

The model equations are

$$N_{i+1} = \lambda N_i g\{N_i\} \left(\alpha + (1 - \alpha) \prod_{q=1}^x f_q \right) \quad (1)$$

$$P_{i,i+1} = \lambda N_i g\{N_i\} (1 - \alpha) (1 - f_i) \prod_{q=1}^{i-1} f_q \quad (2)$$

Here, λ , the basic reproductive rate of the host population, is the number of female host offspring surviving to adulthood in the absence of parasitoids following the introduction of one fecund adult female host. $g\{N_i\}$ is the proportion of hosts surviving intraspecific competition. Competition is assumed to be of the 'contest' type (e.g. Hassell 1978), with $g\{N_i\} = 1/(1 + N_i(\lambda - 1)/Q)$, where Q is the carrying capacity of the host population. The quantity f_i is the constant proportion of hosts escaping parasitism from parasitoid species i . Finally, a proportion α of hosts, completely protected from parasitism over their lifetimes (due to the action of one or more refuges, Fig. 23.1), are assumed to be in the 'total refuge'. We assume that each parasitoid species perceives the same total refuge of the host.

Single parasitoid assemblages

We begin by considering the special case where there is only a single parasitoid species in the assemblage (i.e. $i = x = 1$). The purpose of this is to show the relevance of basic species interactions to some of the patterns generated for large parasitoid assemblages.

Because of some of the simplifying assumptions made in equations 1 and 2, we are able to derive an analytical expression for the host equilibrium, N^* , or

$$N^* = \frac{Q}{\lambda - 1} [\lambda \alpha (1 - f_1) + \lambda f_1 - 1], \quad (3)$$

and, a positive equilibrium point for the host is only possible if

$$\alpha > \frac{1/\lambda - f_1}{1 - f_1}. \quad (4)$$

In other words, the host refuge must be sufficiently large. If the exploitation capacity (i.e. the *per capita* risk of a host being attacked) of the parasitoid is sufficiently small (i.e. $f_1 \geq 1/\lambda$) then even hosts with no refuge persist at positive densities.

At equilibrium, the number of parasitoids produced by the host, $\hat{P}_1$, is given by (from equations 2 and 3)

$$\hat{P}_1 = \frac{Q}{\lambda - 1} \left(\lambda - \frac{1}{\alpha + (1 - \alpha)f_1} \right) (1 - \alpha) (1 - f_1). \quad (5)$$

We now pose the following question: under what conditions would we expect the parasitoid to appear in a host sample and thus be considered present in the host population? Clearly, if the host population were to be sampled in large enough numbers over a sufficiently large area, then one might expect the parasitoid to appear. But, since a host population can rarely be exhaustively sampled, it is more realistic to measure the propensity of a parasitoid species to appear in a sample of a fixed area of habitat.

As expected, the density of hosts increases with the refuge due to the decreasing availability of hosts to the parasitoid (Fig. 23.2). If λ and/or f_1 are sufficiently small then host density is depressed to zero for low levels of refuge. Past a point $\alpha = (1/\lambda - f_1)/(1 - f_1)$, host density increases more or less

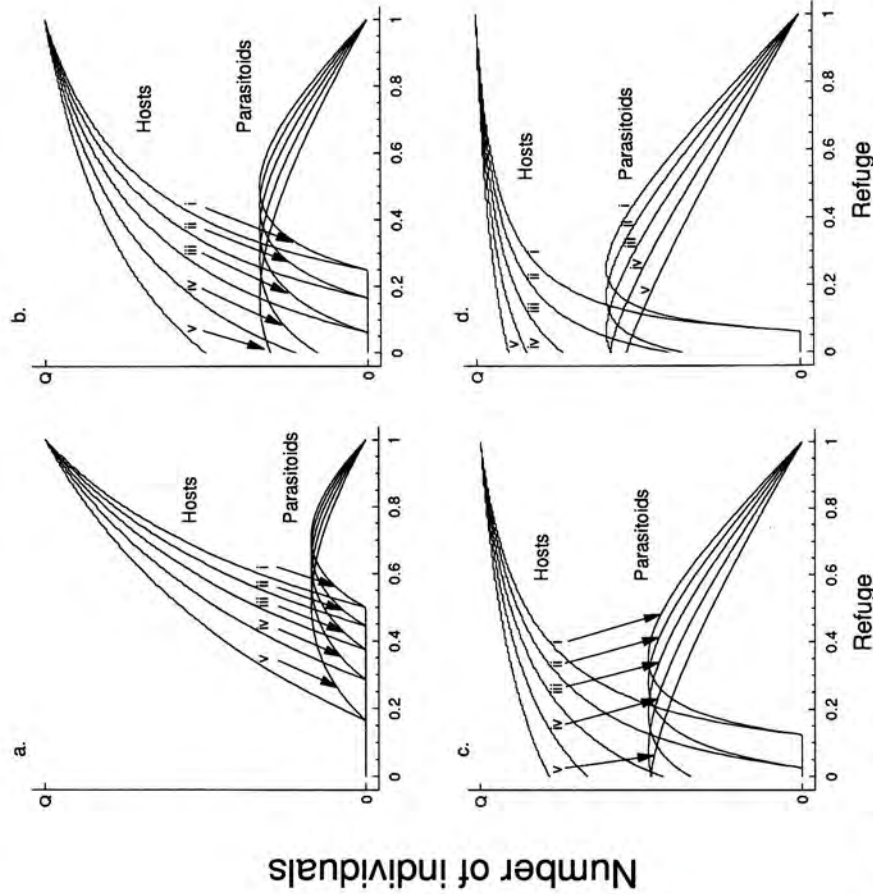


Fig. 23.2 Host and parasitoid abundance for a single species of parasitoid. Host abundance is taken as $\lambda N^* g\{N_i\}$. Numerals i-v indicate special cases by being pointed to the right of corresponding host abundance curves and with an arrow for parasitoid curves. (i) $f_1 = 0.001$, (ii) $f_1 = 0.1$, (iii) $f_1 = 0.2$, (iv) $f_1 = 0.3$, (v) $f_1 = 0.4$. (a) $\lambda = 2$, (b) $\lambda = 4$, (c) $\lambda = 8$, and (d) $\lambda = 16$.

latitudinal gradients in parasitoid community richness as an example. Fourth, we aim to apply our model to the choice of a parasitoid species for release in biological control programmes. We present a criterion, which if met should permit the substantial depression of the herbivore pest population.

The refuge mechanism

We hypothesize that a fixed proportion of hosts is protected from parasitism each generation. A variety of mechanisms may contribute to host protection, including host behaviour and morphology (e.g. Barbosa and Saunders 1985; Gauld *et al.* 1992; Crawley 1992a; Gross 1993), but the extent to which they act through a constant per capita risk of vulnerability to parasitism is unknown.

Figure 23.1 presents one possible representation of how the proportional

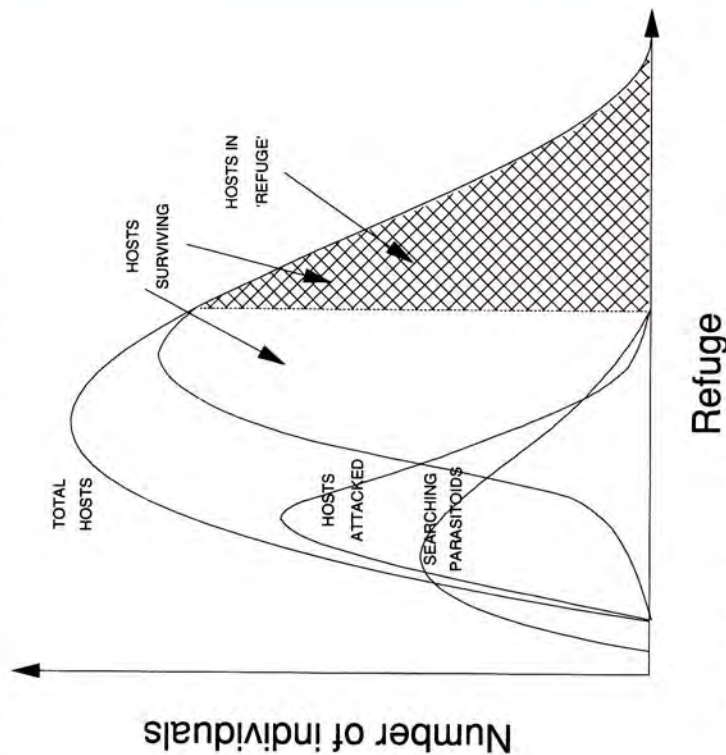


Fig. 23.1 Hypothetical representation of a proportional refuge mechanism. Hosts are distributed along a refuge axis (e.g. depth within a twig) and parasitoids distributed according to their potential access to these hosts (e.g. length of ovipositor). The actual number of hosts attacked is determined by the frequency distribution of parasitoid access to host refuges, spatial heterogeneities in other forms of risk to parasitism, and the smaller attack rates associated with difficulties in access to the refuge. The hatched area represents the constant proportional refuge considered in our model. This assumes the parasitoid access curve is truncated at a maximum access level and the proportion of hosts beyond this access level does not vary with host density.

refuge can work. The horizontal axis represents a quantitative character translating into a barrier to parasitoid attack. Take, for example, depth within a twig or fruit (e.g. Hawkins *et al.* 1987; Compton *et al.* Chapter 18). There is apt to be variation in the depth at which hosts are lodged, and a given population of parasitoids will most readily have access to the least protected hosts. This will be due to phenotypic variation in quantitative traits such as ovipositor size, or the ability of the female parasitoid to detect the presence of deeply lodged hosts. Unless there is sufficient phenotypic diversity in the parasitoid population to enable some individuals potential access to the most protected hosts, there will always be some hosts that are completely invulnerable to the parasitoid, regardless of parasitoid density. Thus, the refuge is inexorably linked to variation in certain phenotypes of both host and parasitoid.

Not all refuges are absolute. 'Probabilistic' refuges (Fig. 23.1), where the risk of attack depends on the local density of searching parasitoids (e.g. May 1978; Chesson and Murdoch 1986; Hassell and Pacala 1990), are complementary to the simpler proportional refuges highlighted in Fig. 23.1, and also can influence the richness of animal assemblages (Shorrocks and Rosewell 1987; Ives 1991; Hochberg and Hawkins 1992, 1993).

The model

To identify the fundamental processes responsible for levels and variation in parasitoid species richness we develop the simplest mathematical expression we can giving rise to patterns produced by more realistic models (Hochberg and Hawkins 1992, 1993). The model differs importantly from past ones by *not* considering the parasitoid populations as dynamic variables and is thus a simplification of one parasitoid—one host models with explicit refuges (e.g. Bailey *et al.* 1961; Hassell and May 1973; Hochberg and Hawkins 1993; Holt and Hassell 1993). This increases the analytical tractability of the system, enabling us to express the results in concise mathematical statements.

The model considers a host with discrete, non-overlapping generations of adult density N_{t+1} at the beginning of generation $t+1$. The host is subject to attack in the larval stages by a pool of x solitary parasitoid species ($1, 2, \dots, i-1, i, i+1, \dots, x$), each inflicting constant levels of mortality (in terms of the per capita risk of a host being attacked) on the host from generation to generation. This assumes each parasitoid population is polyphagous and maintained at more or less constant levels by an assemblage of host species (of which the host considered here is a part), and the parasitoids do not respond numerically to the host. We assume that the parasitoids compete both through exploitative and (pre-emptive) interference mechanisms with species $i-1$ always out-competing species i when larvae of the two co-occur within the same host individual. $P_{i,t+1}$ hosts produce adults of parasitoid species i .

The implications of population dynamics theory to parasitoid diversity and biological control

Michael E. Hochberg and Bradford A. Hawkins

Introduction

Insect parasitoids constitute an important and diverse group of taxa. Recent estimates indicate an average of about five to six parasitoid species per insect herbivore species (Askew and Shaw 1986; Hawkins and Lawton 1987; Hawkins 1990; Mills 1992, Chapter 3), although the range extends to almost 100 species (Delucchi 1982). Explaining this range in richness is an important challenge to community ecology.

Comparative studies have shown how host feeding niche contributes substantially to explaining variation in parasitoid richness (Hawkins and Lawton 1987; Mills 1993; Hawkins 1993a). Feeding niche has been interpreted as a mechanism generating a 'refuge' for those host individuals that are sufficiently (and best) protected from parasitoid attack (Simmonds 1948; Gross 1991; Hawkins and Gross 1992; Hawkins 1993a). Recently, we developed a quantitative theory, based on refuges to parasitism, to explain current levels of parasitoid species richness across host species (Hochberg and Hawkins 1992, 1993). The emphasis was on structural refuges provided by the plants that endophytic hosts infest. We found that while these structural refuges were sufficient to account for the parasitoid species richness–host feeding niche relationship, they could not be used to predict exophytic richness without making further assumptions. In particular, if the model were to include other types of refuge, then the relationship between total refuge and species richness would be in accord with the data.

We have four principal aims. First, we seek to relate our quantitative theory to the larger domain of consumer–resource interactions. How fundamental are the processes that constrain species richness, and how simple can the theory be without altering the conclusions? Second, we want to know the conditions where theory and data coincide. How does incorporating other types of refuges besides the structural ones provided by the host food plant affect the fit of predicted to observed patterns? Third, we hope to demonstrate how the model can be used as a heuristic tool for examining determinants of parasitoid species richness for a wide range of situations, using