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Refuge Theory and Biological Control

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An important question in ecology is the extent to which populations and communities are governed by general rules. Recent developments in population dynamics theory have shown that hosts' refuges from their insect parasitoids predict parasitoid community richness patterns. Here, the refuge theory is extended to biological control, in which parasitoids are imported for the control of insect pests. Theory predicts, and data confirm, that the success of biological control is inversely related to the proportion of insects protected from parasitoid attack. Refuges therefore provide a general mechanism for interpreting ecological patterns at both the community level (their species diversity) and population level (their dynamics).

The practice of introducing parasitoids, those insects that parasitize and kill their arthropod hosts, for the biological control of insect pests has contributed much to ecological theory. Unfortunately, the converse is not true (*1*), because analytical parasitoid-host models that have been applied to biological control (*2*) have not identified simply measured, unambiguous parameters that actually improve the chances of successful pest control. Consequently, the practice of biological control through the introduction of natural enemies remains largely empirical and based on trial and error, in spite of the need to improve its scientific basis (*3*, *4*).

We propose that theory recently developed to account for variability in the species richness of parasitoid communities offers a simple methodology to evaluate the extent to which a parasitoid introduction will control a pest population. The model formalizing the theory (*5*, *6*) identifies proportional refuges from parasitism [defined as a fixed proportion of the host population immune to attack (*7*)] as a key constraint on the number of parasitoid species that can persist on a host (*5*). As a result of its population-dynamic structure, the model further quantifies the extent that parasitoids will depress host populations below the densities hosts would achieve in the absence of parasitoids (*6*).

It is this second property of the model that is relevant to biological control, the goal of which is to reduce and maintain pest populations below some critical density defined as their economic threshold. Basically, refuge theory predicts that hosts that occupy small refuges (that is, a low proportion of their population is in the refuges) will be highly exploitable by parasitoids, and as a result the host populations will be

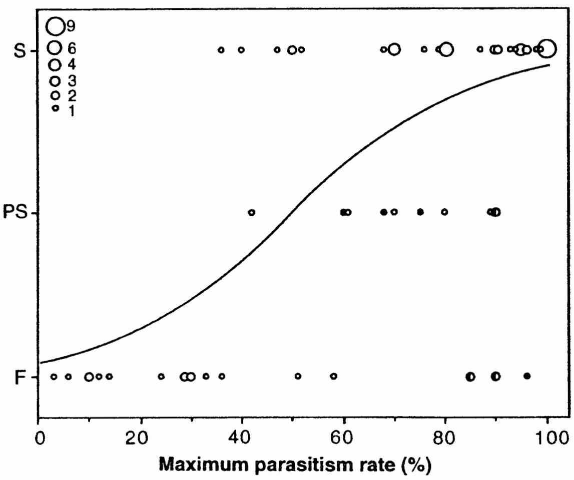

Fig. 1. Relation between maximum percentage parasitism (in two cases including host mortality from host feeding by the parasitoid) and the outcome of parasitoid introductions for classical biological control. Multiple cases are denoted by larger circles. Blackened symbols represent failures and partial successes attributed to climatically related factors. The regression line illustrated is based on a logistic regression when partial successes have been excluded (logit$y$ = $-2.880 + 0.057x$, $\chi^2 = 28.48$, $n = 64$, $P < 0.0000001$). Regressions based on an economic evaluation of success (less than full control considered a failure) and a dynamic evaluation of success (full and partial successes taken as equal evidence of the ability of parasitoids to reduce pest densities) produced similar statistics (logit$y$ = $-2.957 + 0.048x$, $\chi^2 = 23.76$, $n = 74$, $P = 0.0000011$ and logit$y$ = $-2.669 + 0.058x$, $\chi^2 = 29.67$, $P < 0.0000001$, respectively).

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Table 1. List of parasitoid releases for biological control ranked by the maximum parasitism rate (Max.) recorded after parasitoid release and establishment. The outcomes of the introductions are based on information provided in the sources (Ref., reference number). Target species may appear more than once where control attempts have been made at different locations or with more than one parasitoid species. F, failure; PS, partial success; and S, success.

Target species	Parasitoid species	Max. (%)	Outcome	Ref.
Leucoptera coffeella	*Mirax insularis*	3	F	(*11*)
Hypera postica	*Bathyplectes curculionis* + *Tetrastichus incertus*	6	F	(*19*)
Aonidiella aurantii	*Prospaltella perniciosi*	10	F	(*20*)
Mayetiola destructor	*Pediobius metallicus*	10	F	(*11*)
Forficula auricularia	*Bigonicheta setipennis*	12	F	(*21*)
Rhabdoscelus obscurus	*Lixophaga sphenophori*	14	F	(*11*)
Brontispa longissima	*Tetrastichus brontispae*	24	F	(*22*)
Diatraea saccharalis	*Paratheresia claripalpus*	29	F	(*11*)
Neodiprion sertifer	14 native and introduced spp.	29	F	(*11, 23*)
Oryctes rhinocerus	*Scolia ruficornis*	30	F	(*11*)
Cydnia pomonella	*Ascogaster quadridentata*	30	F	(*24*)
Eoreuma loftini	*Allorhogas pyralophagus*	33	F	(*17*)
Brontispa longissima	*Tetrastichus brontispae*	36	F	(*25*)
Nipaecoccus viridis	*Anagyrus indicus* + *A. kamali*	36	S	(*26*)
Operophtera brumata	*Agrypon flaveolatum*	40	S	(*11*)
Acyrthosiphon pisum	*Aphidius eadyi*	42	PS	(*27*)
Cephus pygmaeus	*Collyria calcitrator*	47	S	(*11*)
Aleurocanthus woglumi	*Prospaltella opulenta*	50	S	(*28*)
Plutella xylostella	*Apanteles plutellae*	50	S	(*29*)
Phthorimaea operculella	*Apanteles subandinus*	51	F	(*30*)
Tryporyza nivella	*Isotima javensis*	52	S	(*31*)
Triathaba complexa	3 parasitoid spp.	58	F	(*11*)
Coleophora laricella	*Chrysocharis laricinellae*	60	PS	(*21*)
Popillia japonica	*Tiphia vernalis*	61	PS	(*11*)
Pristiphora erichsonii	*Mesoleius tenthredinis*	68	S	(*32*)
Eriosoma lanigerum	*Aphelinus mali*	68	PS	(*33*)
Lamprosema octasema	*Chelonus stratigenas*	70	PS	(*29*)
Sirex noctilio	3 parasitoid spp.	70	S	(*24*)
Phenacoccus manihoti	*Epdinocarsis lopezi*	70	S	(*34*)
Lepidosaphes beckii	*Aphytis lepidosaphes*	70	S	(*11*)
Proceras sacchariphagus	*Apanteles flavipes*	70	S	(*35*)
Leptinotarsus decemlineata	*Doryphorophaga doryphorae*	75	PS	(*36*)
Laspeyresia nigricana	*Ascogaster quadridentata*	76	S	(*11*)
Brontispa longissima	*Tetrastichus brontispae*	79	S	(*25*)
Phytomyza ilicis	4 parasitoid spp.	80	PS	(*11*)
Operophtera brumata	*Cyzenis albicans*	80	S	(*11*)

severely reduced. Conversely, for hosts that occupy sufficiently large refuges, parasitoids will be unable to exploit the host population sufficiently to appreciably depress its density (*8*). The precise effect of the refuge capacity on host abundance depends on other parameters in the model (notably, the maximum population growth rates of the host and parasitoid), but if the conceptual basis of the theory is correct, measurement of the proportion of the host's population subject to attack should be an important parameter describing the amount of host population depression and thus should provide a reliable estimation of whether a parasitoid will be able to successfully control its host.

We tested this prediction by searching the classical biological control literature for reports of parasitoid introductions that provided field estimates of parasitism and an evaluation of the outcome. Because refuges from parasitism can arise from many sources [including intrinsic, physiologically based host defenses and extrinsic defenses arising from plant structures inhabited by hosts (*9*)], we recorded the maximum parasitism level achieved in any host population as the best estimate of the proportion of hosts not in the refuge (*10*). We identified 74 cases for which the required information was provided (Table 1).

Evaluations of biological control are typically based on economic criteria; a parasitoid introduction either fails to influence the status of the pest or, alternatively, the pest is partially or completely controlled. Because most evaluations of outcomes are nonquantitative, we analyzed biological control three ways, each by logistic regression. (i) We contrasted clear outcomes, those that resulted in complete failures or complete successes. In this test we excluded partial success, cases in which parasitoids reduced pest populations to some extent, but full economic benefits were not realized. (ii) We used a conservative economic criterion, in which partial successes were included and classified as failures. (iii) The final analysis was based on a more optimistic, dynamic criterion for which all successes, whether partial or complete, were pooled and tested against failures. This distinguishes cases in which parasitoids were able to exert at least some control on host densities from cases in which parasitoids were unable to significantly reduce pest densities.

As predicted by theory, there is a strong association between maximum parasitism rates and biological control outcomes (Fig. 1). Moreover, the relation is robust, even when the more conservative, economic criterion for success is applied. Thus, the maximum susceptibility of a host to parasitoid attack (estimated by maximum parasitism rates) provides a highly significant estimate of the probability that the parasitoid introduction will reduce host densities.

Consistent with the population dynamics models on which refuge theory is based (*2, 5, 6*), our results do not identify host

Table 1. (continued).

Target species	Parasitoid species	Max. (%)	Out-come	Ref.	Target species	Parasitoid species	Max. (%)	Out-come	Ref.
Phenacoccus aceris	*Allotropa utilis*	80	S	(*11*)	*Aleurocanthus woglumi*	*Prospaltella opulenta*	93	S	(*11*)
Rhyacionia frustrana	*Campoplex frustranae*	80	S	(*11*)	*Pristiphora geniculata*	*Olesicampe geniculatae*	94	S	(*19*)
Unaspis yanonensis	*Aphytis yanonensis*	80	S	(*37*)	*Oulema melanopus*	*Tetrastichus julis*	95	S	(*19*)
Anastrepha spp.	*Aceratoneuromyia indica*	80	S	(*38*)	*Diatraea saccharalis*	*Lixophaga diatraea*	95	S	(*44*)
Phyllonorycter messaniella	*Apanteles circum-scriptus* +				*Diatraea saccharalis*	*Apanteles flavipes*	95	S	(*44*)
	Achrysocharoides splendens	80	S	(*24*)	*Mythimna separata*	*Apanteles ruficrus*	95	S	(*45*)
Agonoxena argaula	*Brachymeria agonoxenae*	85	F	(*11*)	*Dasyneura mali*	*Prosactogaster demades*	96	F	(*14*)
Anthonomus grandis	*Bracon kirkpatricki*	85	F	(*11*)	*Plutella xylostella*	*Diadegma eucerephaga*	96	S	(*29*)
Antonina graminis	*Neodusmetia sangwani*	87	S	(*39*)	*Agromyza frontella*	*Dacnusa dryas*	96	S	(*46*)
Brontispa mariana	*Tetrastichus brontispae*	89	PS	(*11*)	*Siphoninus phillyreae*	*Encarsia partenopea*	98	S	(*47*)
Carulaspis minima	*Encarsia lounsburyi*	90	F	(*40*)	*Homona coffearia*	*Macrocentrus homonae*	99	S	(*31*)
Caliroa cerasi	*Lathrolestes luteolator*	90	F	(*24*)	*Chromaphis juglandicola*	*Trioxys pallidus*	100	S	(*11*)
Parabemisia myricae	*Eretmocerus debachi*	90	S	(*41*)	*Lepidosaphes ficus*	*Aphytis mytilaspidis*	100	S	(*11*)
Leucoma salicis	*Apanteles solitarius*	90	PS	(*21*)	*Levuana irridescens*	*Bessa remota*	100	S	(*11*)
Parlatoria oleae	*Aphytis maculicornis*	90	PS	(*42*)	*Nezara viridula*	*Trissolcus basalis*	100	S	(*29*)
Rhabdoscelus obscurus	*Lixophaga spenophori*	90	S	(*31*)	*Plutella xylostella*	*Tetrastichus sokolowskii*	100	S	(*29*)
Rastrococcus invadens	*Gyranosoidea tebygi*	90	S	(*43*)	*Promecotheca coeruleipennis*	*Pediobius parvulus*	100	S	(*11*)
Aleurocanthus woglumi	*Eretmocerus serius*	91	S	(*11*)	*Pseudococcus citriculus*	*Clausenia purpurea*	100	S	(*11*)
Coleophora laricella	*Agathis pumila*	91	S	(*11*)	*Maconellicoccus hirsutus*	*Anagyrus kamali*	100	S	(*11*)
					Ceroplastes rubens	*Anicetus annulatus*	100	S	(*48*)

susceptibility as the only factor affecting host population depression. Parasitoid introductions sometimes fail even when maximum parasitism rates are high (Fig. 1). Complete or partial failure can occur for several reasons, including climatic mismatch (*11*), high incidence of hyperparasitism (*12*), extremely low economic thresholds of the pest (*13*), or poor synchrony with the host (*14*). The particular importance of climate to successful biological control is apparent in our data set; 4 of the 10 partial successes and 3 of the 5 clear exceptions to the outcome predicted by the theory involve climatic factors that reduce parasitoid reproduction, survivorship, or host synchrony (Fig. 1). Obviously, these cases are beyond the scope of refuge theory, which assumes that parasitoids are climatically adapted. Exceptions arising from interactions between parasitoids and climate are consistent with the widely recognized basic requirement for good climatic matching (*15*). On the other hand, even including these cases in our analysis does not alter our main conclusion that host susceptibility provides a good estimator of the outcome of classical biological control.

These results are important in at least four ways. (i) They represent a test of theory proposing that refuges from parasitism represent a major constraint on parasitoid-host interactions, thus influencing not only parasitoid community species richness (*5, 6, 16*) but also host population dynamics. (ii) They provide biocontrol workers with an unambiguous parameter that is relatively easy to measure in the field [either during cage studies (*17*) or field trials before general release of the agent, or during post-release evaluations] that may assist them in gauging the potential success of an introduction (*18*). (iii) They suggest that despite the inherent complexities in parasitoid-host systems, relatively simple theory and models can capture the main features of the dynamics. (iv) They suggest that refuges from parasitism provide a mechanistic foundation for the scientific basis of biological control.

REFERENCES AND NOTES

1. J. Waage, in (*4*), pp. 135–157.
2. For recent reviews of the models, see W. W. Murdoch, in (*4*), pp. 1–24; T. H. Jones, M. P. Hassell, R. M. May, in *Parasitoid Community Ecology*, B. A. Hawkins and W. Sheehan, Eds. (Oxford Univ. Press, Oxford, in press).
3. P. DeBach, Ed., *Biological Control of Insect Pests and Weeds* (Chapman & Hall, London, 1964).
4. M. Mackauer, L. E. Ehler, J. Roland, Eds., *Critical Issues in Biological Control* (Intercept, Andover, United Kingdom, 1990).
5. M. E. Hochberg and B. A. Hawkins, *Science* **255**, 973 (1992).
6. ———, *Am. Nat.*, in press.
7. M. P. Hassell, *The Dynamics of Arthropod Predator-Prey Systems* (Princeton Univ. Press, Princeton, NJ, 1978).
8. See also J. R. Beddington, C. A. Free, J. H. Lawton, *Nature* 273, 513 (1978).
9. P. W. Price *et al.*, *Annu. Rev. Ecol. Syst.* **11**, 41 (1980); P Gross, *Annu. Rev. Entomol.* **38**, 251 (1993).
10. B. A. Hawkins, *Am. Nat.* **141**, 634 (1993); M. E. Hochberg and B. A. Hawkins, in *Parasitoid Community Ecology*, B. A. Hawkins and W. Sheehan,

Eds. (Oxford Univ. Press, Oxford, in press). Estimates of percentage parasitism include host mortality resulting from destructive host feeding by parasitoids when it was reported.
11. C. P. Clausen, Ed., *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review*, no. 480 of *Agricultural Handbook* (Department of Agriculture, Washington, DC, 1978), p. 260.
12. ______, *ibid.*, p. 171.
13. ______, *ibid.*, p. 314.
14. D. H. Todd, *N.Z. J. Agric. Res.* **2**, 859 (1959).
15. For a discussion of abiotic factors and biological control, see C. B. Huffaker and P. S. Messenger, in (*3*), pp. 74–177.
16. B. A. Hawkins and P. Gross, *Am. Nat.* **139**, 417 (1992); B. A. Hawkins, in *Hymenoptera and Biodiversity*, J. LaSalle and I. D. Gauld, Eds. (CAB International, Wallingford, United Kingdom, 1993), pp. 235–256.
17. For an example of how field cages can be used to estimate refuges from parasitoid attack, see B. A. Hawkins, H. W. Browning, J. W. Smith Jr., *Entomophaga* **32**, 483 (1987).
18. As an example, our limited data indicate that parasitoids released into field cages that are unable to kill at least 25 to 30% of their hosts, either through parasitism or host feeding or both, have a very low probability of being successful, and it would be prudent to continue searches for more efficient species. Quantifying maximum parasitism rates in field cages could also prove valuable for prioritizing potential agents, allowing the best species or combination of species to be released.
19. J. S. Kelleher and M. A. Hulme, *Biological Control Programmes Against Insects and Weeds in Canada, 1909–1980* (Commonwealth Agricultural Bureaux, Farnham Royal, United Kingdom, 1984).
20. G. O. Furness, G. A. Buchanan, R. S. George, N. L. Richardson, *Entomophaga* **28**, 199 (1983).
21. F. Morris, *Commonw. Inst. Biol. Control Tech. Commun.* **4** (1971).
22. P. Cochereau, *Cah. ORSTOM Ser. Biol.* **7**, 139 (1969).
23. K. J. Griffiths, *Can. Entomol.* **91**, 501 (1959).
24. P. J. Cameron, R. L. Hill, J. Bain, W. P. Thomas, *Commonw. Inst. Biol. Control Tech. Commun.* **10** (1989).
25. S. C. Chiu, P. Y. Lai, B. H. Chen, Z. C. Chen, J. F. Shiau, *J. Agric. Res. China* **34**, 213 (1985).
26. D. E. Meyerdirk, S. Khasimuddin, M. Bashir, *Entomophaga* **33**, 229 (1988).
27. P. J. Cameron, G. P. Walker, D. J. Allan, *N.Z. J. Zool.* **8**, 105 (1981).
28. K. R. Summy and F. E. Gilstrap, *Biol. Control* **2**, 19 (1992).
29. D. R. Waterhouse and K. R. Norris, *Biological Control: Pacific Prospects* (Inkata, Melbourne, 1987).
30. M. A. Foot, *N.Z. J. Zool.* **6**, 623 (1979).
31. V. P. Rao, M. A. Ghani, T. Sankaran, K. C. Mathur, *Commonw. Inst. Biol. Control Tech. Commun.* **6** (1971).
32. J. H. McLeod, *Proc. Entomol. Soc. B.C.* **50**, 19 (1954).
33. D. Greathead, *Commonw. Inst. Biol. Control Tech. Commun.* **7** (1976).
34. P. Neuenschwander and P. Herren, *Philos. Trans. R. Soc. London Ser. B* **318**, 319 (1988).
35. M. Betededer-Matibet and P. Malinge, *Agron. Trop.* **22**, 1196 (1967).
36. G. Tamaki, R. L. Chauvin, A. K. Burditt Jr., *Environ. Entomol.* **12**, 386 (1983).
37. K. Furuhashi and N. Okubo, in *The Use of Natural Enemies to Control Agricultural Pests*, O. Mochida, K. Kiritani, J. Bay-Petersen, Eds. (Food and Fertilizer Technology Center for the Asian and Pacific Region, Tapei, 1990), pp. 71–82.
38. E. Jimenez Jimenez, *Fitofilo* **38**, 34 (1963).
39. U. Gerson, E. Mescheloff, E. Dubitzki, *J. Appl. Ecol.* **12**, 767 (1975).
40. M. J. W. Cock, *Commonw. Inst. Biol. Control Tech. Commun.* **9** (1985).
41. M. Rose and P. DeBach, *Isr. J. Entomol.* **25–26**, 73 (1992).
42. P. DeBach, D. Rosen, C. E. Kennett, in *Biological Control*, C. B. Huffaker, Ed. (Plenum, New York, 1971), pp. 165–194.
43. D. Moore, personal communication.
44. M. M. Alam, F. D. Bennett, K. P. Carl, *Entomophaga* **16**, 151 (1971).
45. M. G. Hill, *J. Appl. Ecol.* **25**, 197 (1988).
46. D. G. Harcourt, J. C. Guppy, F. Meloche, *Environ. Entomol.* **17**, 337 (1988).
47. J. R. Gould, T. S. Bellows Jr., T. D. Paine, *Ecol. Entomol.* **17**, 127 (1992).
48. Y. Hirose, T. Nakamura, M. Takagi, in (*4*), pp. 171–183.
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