

On the elusiveness of enemy-free space: spatial, temporal, and host-plant-related variation in parasitoid attack rates on three gallmakers of goldenrods

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Abstract Host shifting by phytophagous insects may play an important role in generating insect diversity by initiating host-race formation and speciation. Models of the host shifting process often invoke reduced rates of natural enemy attack on a novel host in order to balance the maladaptation expected following the shift. Such “enemy-free space” has been documented for some insects, at some times and places, but few studies have assessed the occurrence of enemy-free space across years, among sites, or among insect species. We measured parasitoid attack rates on three insect herbivores of two goldenrods (*Solidago altissima* L. and *Solidago gigantea* Ait.), with data from multiple sites and multiple years for each herbivore. For each insect

herbivore, there were times and sites at which parasitoid attack rates differed strongly and significantly between host plants (that is, enemy-free space existed on one host plant or the other). However, the extent and even the direction of the attack-rate difference varied strongly among sites and even among years at the same site. There was no evidence of consistent enemy-free space for any herbivore on either host plant. Our data suggest that enemy-free space, like many ecological and evolutionary forces, is likely to operate as a geographic and temporal mosaic, and that conceptual models of host shifting that include enemy-free space as a consequence of host novelty are likely too simple.

Keywords Host shift · Enemy-free space · Parasitoid · Phytophagous insect

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Introduction

The astonishing diversity of phytophagous insects (Mitter et al. 1988) has led to enormous interest in ecological mechanisms that may have driven their diversification. One such mechanism (review Berlocher and Feder 2002) is the differentiation of herbivore lineages attacking different hosts (host-associated differentiation), either in sympatry (e.g., Abrahamson and Weis 1997; Bush and Smith 1998) or in allopatry. In either case, a step that must precede host-associated differentiation is the addition of a new host species to the diet of at least some herbivore individuals—with or without abandonment of the original host. Phylogenetic (Janz and Nylin 1998; Janz et al. 2001), historical (Bush and Smith 1998; Carroll and Boyd 1992) and

niche-breadth (Novotny et al. 2002, 2003) data all imply that such “host shifts” are relatively common.

The occurrence of host shifts, however, poses something of a puzzle. Individuals feeding on a novel host plant should often have lower fitness compared to those feeding on host(s) to which their evolutionary history has suited them (e.g., Berenbaum and Zangerl 1991; Feder 1995). Such maladaptation may be associated with factors such as physical or chemical defense of the novel host (Ehrlich and Raven 1964), the ability of the herbivore to locate and recognize suitable hosts, or phenological mismatching between ancestral herbivore and novel host (e.g., Feder 1998). Alleles conferring acceptance of a novel host, then, should be selected against unless there is some countervailing benefit associated with the shift. One such benefit may be reduced herbivore mortality from parasitoids, predators, or disease on the novel host (Price et al. 1980; Jeffries and Lawton 1984); that is, the novel host may provide “enemy-free space” (EFS).¹ [We adopt here the original and broader definition of EFS (see Schiers and De Bruyn 2002), in preference to the narrower definition of Berdegue et al. 1996; the latter confounds criteria for the existence of EFS with those for its sufficiency as an explanation for host choice.]

Many authors have suggested that the existence of enemy-free space on novel hosts is an important factor permitting host shifts (e.g., Porter 1928; Bush 1974; Price et al. 1980; Jeffries and Lawton 1984; Bernays and Graham 1988). However, there is little evidence bearing on its frequency or importance. In a survey of the literature, we found 38 comparisons of rates of parasitism and/or predation across two or more host plants at the same sites (Table 1), although in most (25) cases it is unknown or unreported which host plant is the novel one. (We were unable to include several additional studies in our compilation because they measured attack rates on herbivores feeding on different host plants in different locations, making it impossible to disentangle spatial and host-plant effects on attack). In seven cases (Table 1A), EFS has been reported on a novel host plant (plus two more cases where EFS has been reported on a plant outside the normal host range; Gratton and Welter 1999; Oppenheim and Gould 2002). However, in other cases shifts onto novel hosts appear to make little difference to parasitoid attack (Gross and Price 1988, for two herbivores), or attack rates can even be higher on the

novel host (Sumerford and Abrahamson 1995; Zangerl et al. 2002). The mixed results of these few comparisons (and the unknown number of unpublished negative results) leave considerable doubt about whether EFS is a common result of host shifting.

Another important dimension of EFS is its consistency (or variability) in space and time. If EFS is to play an important role in facilitating host shifts, it likely needs to remain available for many generations until initial maladaptation to the novel host can be overcome by selection. In addition, EFS will be most effective in facilitating host shifts if it is spatially widespread, at least relative to the scale of dispersal by the herbivores. For several reasons, the selective effect of enemy-free space may resemble a geographic and/or temporal mosaic (Thompson 1994, 1997) rather than a simple parasitoid-escape advantage. After all, attack by parasitoids and predators on a given herbivore is often highly variable in space and time (e.g., Feeny et al. 1985; Mira and Bernays 2002; Stireman and Singer 2002; Singer and Stireman 2003; Kumpulainen et al. 2004; Singer et al. 2004), and if nothing else EFS cannot exist at sites or times where attack is negligible on either host (e.g., Mira and Bernays 2002). Furthermore, parasitoids of herbivores with host races or cryptic species on alternative hosts may themselves have evolved specialist races or species (Stireman et al. 2006) with the potential for independently varying population dynamics.

Existing data are far too scanty for a useful assessment of spatial and temporal consistency of EFS. Most studies of EFS compare attack between hosts at a single site, or a few nearby sites, and in a single year (Table 1, and see Schiers and De Bruyn 2002). For example, of the 38 tests for EFS in Table 1, just 11 include data from more than one site: four of these failed to analyze spatial variability in EFS, one found no EFS anywhere, and the remaining six found EFS to vary significantly in space. Of 13 studies that measured EFS in two different years, one did not analyze the year effect and one found no EFS at any time; of the remainder, seven found EFS consistent in direction and strength, while four did not. Only four studies measured EFS through more than 2 years, with two finding consistency through time, and two finding variability. The data are even more limited if we restrict our attention to studies of herbivores with a known novel host (Table 1A): just three studies measured EFS at more than one site (with none finding EFS consistent across sites), and just three studies measured EFS at the same sites through time (consistent EFS through 2–4 years, but not always on the novel host). In summary, there are currently few data meeting the

¹ The term “enemy-free space” is unfortunate, because we doubt that any host ever provides complete escape from enemies. “Enemy-reduced space” would be a better term, but we retain the more familiar phrasing.

Table 1 Spatial and temporal extent of literature studies of enemy-free space

Study	Herbivore	Hosts	Does EFS exist? ^a	Is EFS on the novel host?	Number of years	Is EFS consistent in time?	Number of sites (extent)	Is EFS consistent in space?
(A) Identity of novel host known								
Auerbach and Simberloff (1988)	All leafminers	<i>Quercus nigra</i> , <i>Q. acutissima</i> , <i>Castanea crenata</i>	Yes	Yes	1		1	
Gross and Price (1988)	<i>Tildenia inconspicuellla</i>	<i>Solanum carolinense</i> , <i>S. melongena</i>	No	–	1		1	
Gross and Price (1988)	<i>Tildenia georgia</i>	<i>Physalis heterophylla</i> , <i>Solanum carolinense</i>	No	–	1		1	
Mulatu et al. (2004)	<i>Phthorimaea operculella</i>	<i>Lycopersicon esculentum</i> , <i>Solanum tuberosum</i>	Yes	Yes	1		1	
Johnson and Siemens (1991)	<i>Stator vachelliae</i>	<i>Acacia flexuosa</i> , <i>Par-kinsonia aculeata</i>	Yes	Yes	1		1	
Oppenheim and Gould (2002)	<i>Heliothis virescens</i>	<i>Physalis angulata</i> , <i>Nicotiana tabacum</i>	Yes	Yes	1		1	
Oppenheim and Gould (2002)	<i>Heliothis virescens</i> / <i>subflexa</i>	<i>Physalis angulata</i> , <i>Nicotiana tabacum</i>	Yes	Yes	1		1	
Sumerford and Abrahamson (1995)	<i>Eurosta solidaginis</i>	<i>Nicotiana tabacum</i> , <i>Solidago gigantea</i> , <i>S. altissima</i>	Yes	No	1		2 ^{b, c}	No
Brown et al. (1995)	<i>Eurosta solidaginis</i>	<i>Solidago gigantea</i> , <i>S. altissima</i>	Yes	Yes	1		3 ^{b, c}	No
Feder (1995)	<i>Rhagoletis pomonella</i>	<i>Malus punila</i> , <i>Crataegus spp.</i>	Yes	Yes	2	No ^d	1	
Mira and Bernays (2002)	<i>Manduca sexta</i>	<i>Datura wrightii</i> , <i>Proboscidea parviflora</i>	Yes	Yes	2	Yes	6 (100 km)	No
Gratton and Welter (1999)	<i>Lirionomyza helianthi</i>	5 spp. Asteraceae	Yes	Yes	3	No	1 per year	
Zangerl et al. (2002)	<i>Depressaria pastinacella</i>	<i>Pastinaca sativa</i> , <i>Heracleum lanatum</i>	Yes	No	4	Yes	1	
(B) Identity of novel host not known								
Auerach and Alberts (1992)	<i>Phyllonorycter salicifoliella</i>	3 spp. <i>Populus</i>	No		1		1	
Ballabeni et al. (2001)	<i>Oreina elongata</i>	<i>Aenostyles allariae</i> , <i>Cirsium spinosissimum</i>	Yes		1		1	
Benrey and Denno (1997)	<i>Pieris rapae</i>	<i>Brassica oleracea</i> , <i>Tropaeolum majus</i> , <i>Lunaria annua</i> , <i>Cleome spinosa</i>	Yes		1		1	
Ohzaki and Sato (1994)	<i>Pieris napi</i>	<i>Arabid gemmifera</i> , <i>A. flagellosa</i>	No		1		1	
Ohzaki and Sato (1994)	<i>Pieris melete</i>	5 spp. Cruciferae	Yes		1		1	
Ohzaki and Sato (1994)	<i>Pieris rapae</i>	4 spp. Crucifera	No		1		2 (12 km)	–
Suckling et al. (2001)	<i>Epiphyas postvittana</i>	<i>Malus domestica</i> , <i>Trifolium repens</i> , <i>Populus nigra</i> , <i>Cytisus scoparius</i>	Yes		1		1	
Vencl et al. (2005)	<i>Chelymophra alterans</i>	<i>Merremia umbellata</i> , <i>Ipomoea phillomega</i>	No		1		1	
Rank and Smiley (1994)	<i>Chrysomela aeneicollis</i>	<i>Salix orestera</i> , <i>S. geveryana</i>	Yes		1		1	
Rossiter (1987)	<i>Lymantria dispar</i>	<i>Quercus spp.</i> , <i>Pinus rigida</i>	Yes		1		2 (550 km)	No
Young and Price (1975)	<i>Heliothis zea</i>	Alfalfa, cotton, sorghum	Yes		1		20 (15 km)	NR
Blair et al. (2005)	<i>Mordellistena convicta</i>	<i>Solidago gigantea</i> , <i>S. altissima</i>	Yes		1		NR	NR

Table 1 continued

Study	Herbivore	Hosts	Does EFS exist? ^a	Is EFS on the novel host?	Number of years	Is EFS consistent in time?	Number of sites (extent)	Is EFS consistent in space?
Fritz et al. (1997)	<i>Phyllonorycter salicifoliella</i>	<i>Salix sericea</i> , <i>S. eriocephala</i>	Yes		2	No	1	
Gänge (1995)	<i>Pterocallis alni</i>	<i>Alnus glutinosa</i> , <i>A. incana</i>	Yes		2	Yes	1	
Hägström and Larsson (1995)	<i>Galerucella lineola</i>	<i>Salix viminalis</i> , <i>S. dasyclados</i>	Yes		2	No	1	
Kagata and Ohgushi (2001)	<i>Paraleucoptera sinuella</i>	<i>Salix miyabeana</i> , <i>Populus sieboldii</i>	No		2	–	1	
Rabb and Bradley (1968)	<i>Manduca sexta</i>	4 spp. Solanaceae	Yes		2	Yes	1	
Yamaga and Ohgushi (1999)	<i>Epilachna pustulosa</i>	<i>Cirsium kamischaticum</i> , <i>Caulophyllum robustum</i>	Yes		2	Yes	1	
Preszler and Boecklen (1994)	<i>Phyllonorycter</i> sp.	<i>Quercus grisea</i> , <i>Q. gambelli</i>	Yes		2	No	2 (160 km)	No
Fritz and Kaufman (1993)	<i>Phyllocolpa nigrita</i>	<i>Salix sericea</i> , <i>S. eriocephala</i> , <i>S. discolor</i>	Yes		2	Yes	2 (6 km)	NR
Fritz and Kaufman (1993)	<i>Phyllocolpa</i> sp. “M”	<i>Salix sericea</i> , <i>S. eriocephala</i> , <i>S. discolor</i>	Yes		2	Yes	2 (6 km)	NR
Zvereva and Rank (2003)	<i>Chrysomela lapponica</i>	<i>Salix borealis</i> , <i>S. caprea</i> , <i>S. phylicifolia</i>	Yes		2	Yes	NR	
Zvereva and Rank (2003)	<i>Chrysomela lapponica</i>	<i>Salix borealis</i> , <i>S. caprea</i> , <i>S. phylicifolia</i>	Yes		2	NR	NR	
Le Corff et al. (2000)	All Lepidoptera	<i>Quercus alba</i> , <i>Q. velutina</i>	Yes		3	No	9 (15 km)	No
Barbosa et al. (2001)	All Macrolepidoptera	<i>Acer negundo</i> , <i>Salix nigra</i>	Yes		5	Yes	4–6 (120 km)	NR

We include studies here only if they compared rates of parasitism or predation, in the field, on one herbivore species (or a pair of sister species) on two or more different host plants at the same site(s). We excluded studies (Mopper et al. 1984; Keese 1997; Murphy 2004) measuring attack on herbivores on one host plant at one site, and on another host plant at a different site. Such studies cannot separate spatial and host-related differences in attack. We searched for studies (term = “enemy” AND “free” AND “space”) in both Biological Abstracts (1989–2005) and Web of Science (1974–2005). We found additional studies via citations in located studies and in Berdegue et al. (1996) and Scheirs and de Bruyn (2002). A more detailed version of this table is available on request from the corresponding author

NR not reported

^a EFS exists if natural enemy attack is significantly less on herbivores on one host plant

^b These studies included additional sites at which only one host plant occurred

^c We reanalyze data from these studies, together with our own, in this paper

^d EFS consistent in direction, but not in intensity (over fivefold difference in one year, twofold in another)

requirements for a full test of the EFS-host shifting hypothesis, but what data we have so far suggest that temporal and spatial variability in EFS may arise rather frequently.

The typical persistence time of EFS following a host shift is also unknown. If a novel host offers EFS because it is intrinsically unsuitable for parasitoid or predator attack, then the EFS benefit of the host shift may be permanent and accrue equally to any herbivore on that host. For example, the shift by the apple

maggot fly, *Rhagoletis pomonella*, from hawthorn to apple affords escape from parasitoids because the size of apples lets flies feed far deeper inside fruits than parasitoid ovipositors can reach (Feder 1995; see also Gruenhagen and Perring 2001; Oppenheim and Gould 2002). In contrast, if a novel host offers EFS only because it is novel and there is a lag in the evolution of parasitoid or predator searching behavior, then EFS might represent only a transitory phase in host shifting (Grosman et al. 2005). Such transitory EFS might not

Table 2 Collection sites, data sources, and dates

Herbivore species	Site name ^a	Location or data source ^b	Collection date
<i>E. solidaginis</i>	Ascutney, VT	Data: Brown et al. (1995) (site CR14). 43°25' N, 72°25' W. Attack rates recalculated from original data	1993
	Chester, VT	Data: Brown et al. (1995) (site CR16). 43°16' N, 72°35' W. Attack rates recalculated from original data	1993
	Bellows Falls, VT	Data: Brown et al. (1995) (site CR18). 43°08' N, 72°27' W. Attack rates recalculated from original data	1993
	Swanton, VT	Old fields in Missisquoi National Wildlife Refuge, Swanton, VT, USA. 44°57' N, 73°13' W	May 2004
	Pellston, MI	Data: Abrahamson et al. (1994), their Fig. 4 (site BS MI). 45°34' N, 84°46' W. Attack rates recalculated from original data	1989
	Menominee, MI	Data: Abrahamson et al. (1994), their Fig. 4 (site ME MI). 45°08' N, 87°38' W. Attack rates recalculated from original data	1989
	Castle Rock, IL	Data: Abrahamson et al. (1994), their Fig. 4 (site CR IL). 41°58' N, 89°23' W. Attack rates recalculated from original data	1989
	Ames, IA	Data: Abrahamson et al. (1994), their Fig. 4 (site 50 IA). 42°02' N, 93°36' W. Attack rates extracted from figure	1989
	Saint Paul, MN	Data: Abrahamson et al. (1994), their Fig. 4 (site CA2 MN). 45°20' N, 93°05' W. Attack rates extracted from figure	1989
	Saint Paul, MN	Data: Abrahamson et al. (1994), their Fig. 4 (site CA1 MN). 45°20' N, 93°05' W. Attack rates recalculated from original data	1991
<i>G. gallaesolidaginis</i>	Fredericton, NB	Fields and open areas along trails north of walking bridge over Saint John River, Fredericton, NB, Canada. 45°57' N, 66°38' W	September 2002, September 2003, September 2004
	Toronto, ON	Old fields and forest edges, Tommy Thompson Park, Toronto, ON, Canada. 43°41' N, 79°18' W	August 2004
	Jackson, TN	Old fields near Cypress Grove Nature Park, west of Jackson, TN, USA. 35°35' N, 88°50' W	September 2001
	Milaca, MN ^c	Old fields along US Highway 169 at Milaca, MN, USA. 45°43' N, 93°37' W	September 2001
	Fort Dodge, IA	Tallgrass prairie in Liska-Stanek Prairie State Preserve, south of Fort Dodge, IA, USA. 42°25' N, 94°13' W	September 2004
	Ames, IA	Tallgrass prairie in McFarland Park, northeast of Ames, IA, USA. 42°05' N, 93°34' W	September 2004
	Lone Tree, IA	Old fields at Cone Marsh Wildlife Management Area, south of Lone Tree, IA, USA. 41°24' N, 91°24' W	September 2000 September 2001
<i>E. scudderiana</i>	Swanton, VT	Missisquoi National Wildlife Refuge, Swanton, VT, USA. 44°57' N, 73°13' W	September 2004
	Toronto, ON	Old fields and forest edges, Tommy Thompson Park, Toronto, ON, Canada. 43°41' N, 79°18' W	October 2003 October 2004
	Milaca, MN ^c	Old fields along US Highway 169 at Milaca, MN, USA. 45°43' N, 93°37' W	December 2002 December 2003 December 2004

^a Two-letter abbreviation: US state or Canadian province

^b Entries beginning with "Data:" refers to datasets reanalyzed from the literature (nine of the ten *Eurosta* datasets). Attack rates were either extracted from specified figures (two datasets) or recalculated from original data provided by one of us (JLB)

^c Approximately 3 km from the "Bogus Brook" site of Nason et al. (2002)

be easily detectable, but could still be critical to host shifting and the rapid evolution of distinct, genetically isolated host forms. One way to address the issue of temporal persistence is to compare EFS for herbivores representing recent and older host shifts across the same pair of host plants, but to our knowledge no such comparisons have been available.

We sought to address these questions by testing for the presence of EFS in parasitoid attack and for its consistency in time and space for three gallmaking insect herbivores of the common goldenrods *Solidago altissima* and *Solidago gigantea*. We confine our analyses to parasitoids, excluding attack by predators or diseases. However, we retain the familiar term “enemy-free space” while emphasizing that we present data for an important guild of enemies, but not for all enemies. Each of our three herbivores has most likely made a host shift from *S. altissima* to *S. gigantea*, but they differ in their degree and history of host specialization: one is a recent host-race pair (*Eurosta solidaginis*; Abrahamson and Weis 1997), another an older cryptic species pair (*Gnorimoschema gallaesolidaginis*; Stireman et al. 2005), and the third a host generalist (*Epiblema scudderiana*; Stireman et al. 2005). These herbivores differ in gall architecture and phenology, and are attacked by different suites of parasitoid species. For each herbivore, we report estimates of parasitoid attack rates for populations distributed over substantial portions of its geographic range (>1,500 km) and collected in several different years. No study to date has reported EFS data for any herbivore for such spatially and temporally extensive collections (Table 1). Our results document important spatial and temporal variability in parasitoid EFS for each herbivore.

Methods

The study system

Our three gallmakers are all herbivores of the common goldenrods *S. altissima* and *S. gigantea* (Asteraceae). These species are closely related (both members of the *S. canadensis* complex in *Solidago* subsection *Triplinervae*), morphologically similar, and broadly sympatric over much of the United States and southern Canada (USDA NRCS 2002). They frequently grow in thoroughly intermixed stands in prairie, meadow, old-field and wetland habitats. They are host to over 100 different insect herbivores (Maddox and Root 1990; Root and Cappuccino 1992; Fontes et al. 1994), of which some are relative generalists attacking either host,

some are pairs of host races with partial reproductive isolation, and others are pairs of cryptic host-specialist species (Stireman et al. 2005).

We report levels of parasitoid attack on the following three gallmakers: the goldenrod ball-gall fly *Eurosta solidaginis* (Diptera: Tephritidae), the goldenrod elliptical-gall moth *Gnorimoschema gallaesolidaginis* (Lepidoptera: Gelechiidae), and the goldenrod spindle-gall moth *E. scudderiana* (Lepidoptera: Tortricidae). *Eurosta* is composed of *S. altissima* and *S. gigantea* host races (Abrahamson and Weis 1997) that are of relatively recent origin (Stireman et al. 2005), with significant genetic differentiation and substantial host fidelity, but likely with ongoing gene flow (Itami et al. 1998). The ancestral host is *S. altissima*, with the *S. gigantea* race derived and likely of northeastern US origin (Waring et al. 1990; Brown et al. 1996). *Eurosta*'s higher mortality on *S. gigantea* early in gall formation suggests a lesser ability to counteract plant defenses on that host (Lichter et al. 1990; Brown et al. 1995). *Gnorimoschema* includes a somewhat older pair of host forms with stronger genetic differentiation and little gene flow (Nason et al. 2002; Stireman et al. 2005); these forms are probably best viewed as host-specialist cryptic species. As is the case with *Eurosta*, the *S. gigantea* host form of *Gnorimoschema* appears to be derived (within-host-form genetic variation is much greater for *Gnorimoschema* on *S. altissima*; Nason et al. 2002; Stireman et al. 2005). *Epiblema*, unlike the other two gallmakers, appears to be a single host generalist attacking either goldenrod (Stireman et al. 2005). Which host plant was more recently added to *Epiblema*'s host range is unknown, but larvae appear more poorly adapted to attacking *S. gigantea* (attaining smaller masses on *S. gigantea* versus *S. altissima* stems of similar size; J.O. Stireman, unpublished data). Since *S. gigantea* is the novel and/or less suitable host for each gallmaker, reduced parasitoid attack on *S. gigantea* for all three gallmakers would support the EFS-in-host-shifting hypothesis.

Field sites and collections

For *Eurosta*, we report data from one new set of collections from Swanton, VT, along with previously published but reanalyzed data (Table 2). Where those published datasets reported *Eurosta* mortality from the facultative inquiline/predator *Mordellistena convicta* (Coleoptera: Mordellidae) and other sources (e.g., undiagnosable predators and birds), we excluded this from mortality estimates to arrive at a parasitoid attack rate (although none of our major conclusions would differ if they had included these other sources of

mortality). For the other two herbivores, all data reported here are previously unpublished.

We collected galls from field sites across the central and northeastern United States and eastern Canada between 2000 and 2004 (Table 2). We chose sites at which both host species were present in large numbers, and at which galls of the targeted herbivore were common on both host species. We then collected galls haphazardly, being careful to avoid preferring larger or more conspicuous galls. For *Eurosta*, we collected galls

in spring, after overwintering and before adult emergence. For *Gnorimoschema*, we collected galls in early autumn, well into moth pupation, but before adult emergence. For *Epiblema*, we collected galls in autumn or winter (before pupation and adult emergence in spring, but while host plants were still easily identifiable to species).

Collected galls were returned to the laboratory for processing. For each gall, the host plant species was determined using stem pubescence (Semple et al.

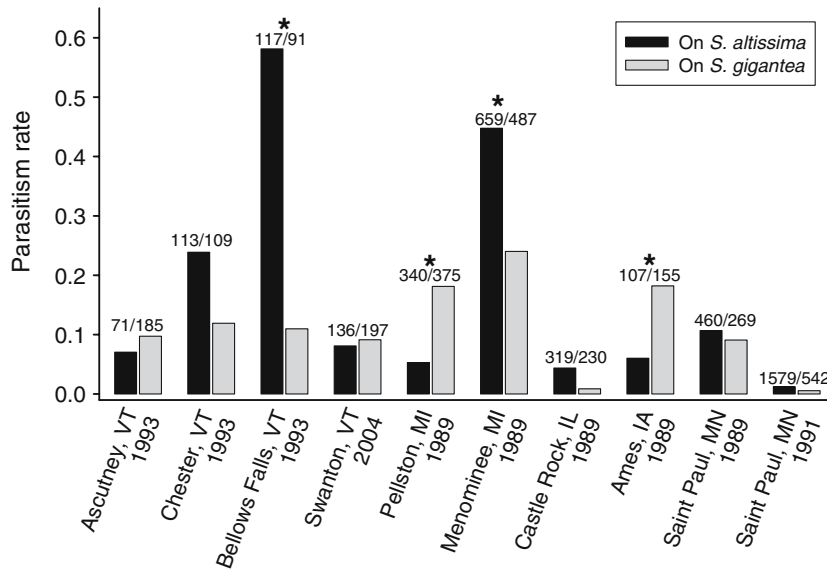
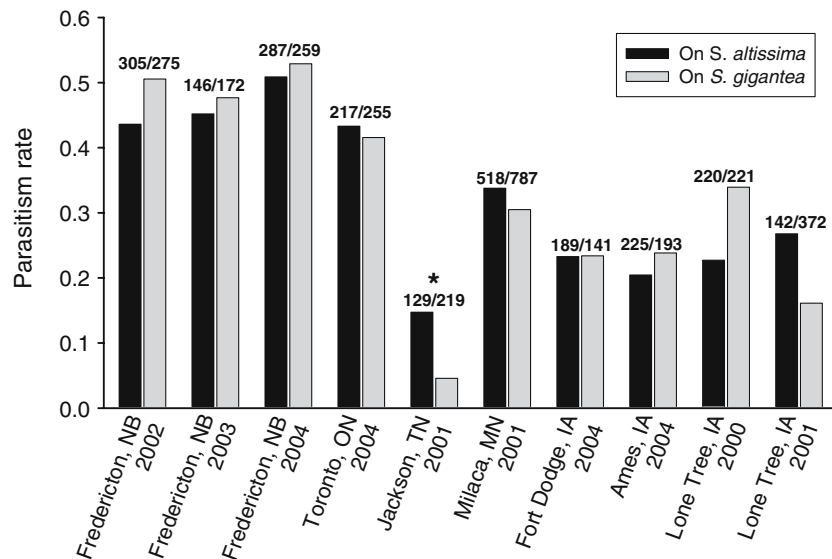


Fig. 1 Parasitoid attack rates on the goldenrod ball-gall fly (*Eurosta solidaginis*) at nine sites (ten site-year combinations). Except for Swanton, VT, all data are extracted from the literature (see [Methods](#): *Eurosta* data). Asterisks indicate significant enemy-free space (EFS) after Bonferroni correction

across site/year combinations; EFS occurs when herbivores on one host experience reduced mortality from parasitoid attack. Numbers above bars are sample sizes (total number of galls surveyed for parasitoids, *S. altissima*/*S. gigantea*). Details of site-by-site statistical analyses are given in Appendix I

Fig. 2 Parasitoid attack rates on the goldenrod elliptical-gall moth (*Gnorimoschema gallaesolidaginis*) at seven sites (ten site-year combinations). Asterisks indicate significant EFS after Bonferroni correction across site/year combinations. Numbers above bars are sample sizes (total number of galls surveyed for parasitoids, *S. altissima*/*S. gigantea*). Details of site-by-site statistical analyses are given in Appendix I



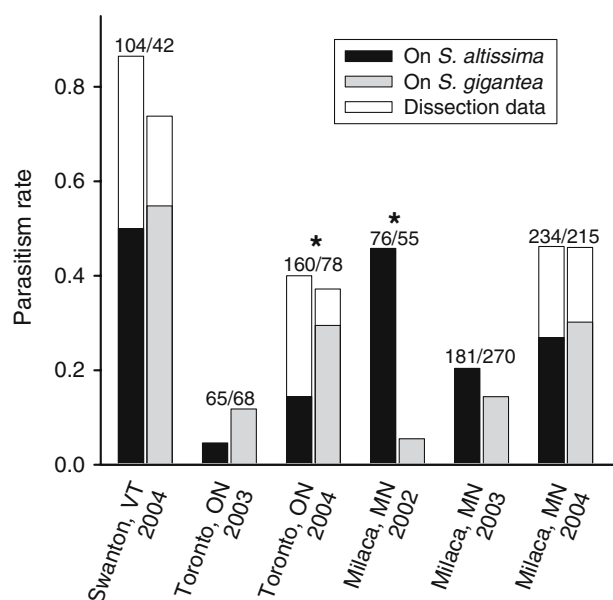


Fig. 3 Parasitoid attack rates on the goldenrod spindle-gall moth (*Epiblema scudderiana*) at three sites (six site-year combinations). Black and grey bars show incidence of parasites discovered before larval dissections; open bars add parasites discovered during larval dissections. Asterisks indicate significant EFS (in pre-dissection data) after Bonferroni correction across site/year combinations. Numbers above bars are sample sizes (total number of galls surveyed for parasitoids, *S. altissima*/*S. gigantea*). Details of site-by-site statistical analyses are given in Appendix I

1999), under a dissecting microscope if necessary. For *Eurosta*, galls were maintained in plastic tubs (with mesh inserts for ventilation) until emergence of adult flies and parasitoids had ceased. For *Gnorimoschema* and *Epiblema*, galls were opened and the occurrence of larval, pupal, or adult gallmakers and parasitoids was recorded. One recorded parasitoid of *Gnorimoschema*, *Tetrastichus paracholus* (Hymenoptera: Eulophidae), matures inside the *Gnorimoschema* pupal case and was therefore missed by our scoring; however, separate rearings of *Gnorimoschema* pupae suggest that *Tetrastichus* is quite uncommon (at least at our Iowa and New Brunswick sites; S.B. Heard, unpublished data). For *Epiblema*, some caterpillars at the prepupal stage we scored will have internal parasitoids, such as the braconid *Macrocentrus pallisteri*, which do not emerge until the following spring (Darling and Gibson 2000). For three collections (2004 collections from Swanton, VT; Toronto, ON; Milaca, MN), we dissected caterpillars and scored them for the occurrence of internal parasitoids. A handful of caterpillars could not be dissected, and we assumed that parasites occurred in those at the same frequency as in the dissected individuals, although none of our conclusions depend on this adjustment. Pre-dissection and postdissection esti-

Table 3 Analysis of *Eurosta* parasitoid attack rates across sites in (A) 1989 and (B) 1993

Source	df	χ^2	P
(A) 1989			
Host	1	0.01	0.92
Site	4	241	<0.0001
Site \times host	4	75	<0.0001
(B) 1993			
Host	1	15	0.0001
Site	2	22	<0.0001
Site \times host	2	20	<0.0001

mates of parasitism provide lower and upper bounds, respectively, on the actual mortality rate to parasitoids (because we could not predict the fate of internal parasitoids, some of which were still small and might not have developed to kill the caterpillar). We analyze both pre- and post-dissection data where available.

For all gallmakers, parasitoids were sorted to species, but we analyze primarily the total attack rate by all parasitoids on a given gallmaker: this is the attack rate most relevant to selection by parasitoids on gallmaker host choice. However, at least for *Eurosta* and *Gnorimoschema*, our major conclusions would be unaltered if we analyzed instead the attack rate by the most common single parasitoid (*Eurytoma gigantea* (Eurytomidae) and *Copidosoma gelechia* (Encyrtidae), respectively).

Data analysis

We tested for the existence of EFS for each gallmaker species separately, because each represents a phylogenetically independent case of host shifting. For each collection (site/year combination) of each gallmaker species, we calculated the total parasitoid attack simply as the number of parasitized individuals divided by the total number of galls collected. Enemy-free space exists when attack is significantly lower on one host than the other. Our analyses address two basic questions: first, whether enemy-free space existed for gallmakers

Table 4 Analysis of *Gnorimoschema* parasitoid attack rates across sites in (A) 2001 and (B) 2004

Source	df	χ^2	P
(A) 2001			
Host	1	18	<0.0001
Site	2	72	<0.0001
Site \times host	2	9.4	0.009
(B) 2004			
Host	1	0.24	0.62
Site	3	118	<0.0001
Site \times host	3	0.87	0.83

Table 5 Analysis of *Gnorimoschema* parasitoid attack rates over time at (A) Fredericton, NB, and (B) Lone Tree, IA

Source	df	χ^2	P
(A) Fredericton, NB			
Host	1	1.26	0.16
Year	2	1.95	0.18
Host \times year	2	3.47	0.67
(B) Lone Tree, IA			
Host	1	0.07	0.79
Year	1	5.75	0.017
Host \times year	1	14.1	0.0002

on either the novel or the ancestral plant host in any given collection; second, whether the extent of enemy-free space and/or the host providing it varied across sites or years. We conducted contingency table analyses (gallmaker fate vs. host plant, site, and/or year) using linear-model analysis in SAS version 8.0 PROC CATMOD (SAS Institute, Cary, NC). We adopted a three-step analysis for each gallmaker because our sampling scheme (not all sites sampled in all years) precluded conducting a single large factorial analysis.

First, we tested for the existence of enemy-free space for each collection separately (EFS = significant host effect in a one-way contingency table analysis). Because we tested multiple collections for each gallmaker, we used a sequential Bonferroni procedure (Rice 1989) to control overall (per-gallmaker) type I error rate.

Second, we tested for spatial variability in enemy-free space using two-way (host and site) contingency table analyses of data collected from multiple sites in the same year. For *Eurosta*, we had data from five sites in 1989 and four in 1993; for *Gnorimoschema*, we had data from three sites in 2001 and four in 2004; for *Epiblema*, we had data for two sites in 2003 and three in 2004 (Table 2). Here, we are most interested in the site \times host interaction, which tests for spatial variation in EFS within a year. An alternative analysis using data from all sites (but not necessarily in the same year) would greatly extend the spatial extent of our tests, but would partly confound temporal with spatial variation. Such an analysis reaches identical conclusions to the within-year analysis (results not reported).

Third, we tested for temporal variation in enemy-free space using two-way contingency table analyses (this time, host and year) of data collected in multiple years at the same site. There were two such sites for *Gnorimoschema* and *Epiblema*, and one for *Eurosta*. Here, we are most interested in the year \times host interaction, which tests for temporal variation in EFS within a site.

Table 6 Analysis of *Epiblema* parasitoid attack rates across sites in (A) 2003 and (B) 2004 (predissection data)

Source	df	χ^2	P
(A) 2003			
Host	1	0.63	0.43
Site	1	6.5	0.011
Site \times host	1	3.7	0.054
(B) 2004			
Host	1	2.8	0.095
Site	2	53	<0.0001
Site \times host	2	2.8	0.25

Results

For all three gallmakers, attack rates differed between galls on *S. altissima* and *S. gigantea* in at least some sites and years (Figs. 1, 2, 3; although for *Epiblema*, there were significant attack rate differences only for our more voluminous predissection data; see below). Importantly, for all three species enemy-free space varied conspicuously from site to site and year to year, with changes in the magnitude of the attack-rate difference and even in which host provided EFS.

Eurosta solidaginis

Attack rates on *Eurosta* ranged from 0.5% (Saint Paul, MN, 1991, *S. gigantea*) to 58% (Bellows Falls, VT, *S. altissima*). Gallmakers on *altissima* had lower attack rates in four cases, and gallmakers on *gigantea* had lower attack rates in six cases (Fig. 1; Appendix I), although many of these differences were not statistically significant after Bonferroni correction. Differences in attack rate were more likely to be significant when overall attack rates were high (Fig. 1, Appendix I), likely because when attack rates are low, very large collections of galls are necessary to attain high statistical power in a test for EFS. Attack rates were significantly lower on the novel host *S. gigantea* at Bellows Falls, VT, and Menominee, MI but on the

Table 7 Analysis of *Epiblema* parasitoid attack rates over time at (A) Toronto, ON, and (B) Milaca, MN

Source	df	χ^2	P
(A) Toronto, ON			
Host	1	6.2	0.013
Year	1	9.4	0.002
Host \times year	1	0.02	0.90
(B) Milaca, MN			
Host	1	17	<0.0001
Year	2	17	0.0002
Host \times year	2	19	<0.0001

ancestral host *S. altissima* at Pellston, MI and Ames, IA (Fig. 1).

In both 1989 and 1993, the direction and extent of EFS varied strongly and significantly among sites (Table 3, host \times site interactions). In light of these strong interactions, we do not interpret tests of the host and site main effects.

Data for 2 years at St. Paul, MN, showed a significant change in parasitoid attack over time ($\chi^2_{(1)}=58$, $P<0.0001$), but no change in relative attack on the two hosts (year \times host $\chi^2_{(1)}=0.75$, $P=0.39$).

Gnorimoschema gallaesolidaginis

Attack rates on *Gnorimoschema* (Fig. 2) ranged from 4.5% (Jackson, TN, *S. gigantea*) to 53% (Fredericton, NB, 2004, *S. gigantea*). Gallmakers on *altissima* had lower attack rates in six cases, and gallmakers on *gigantea* had lower attack rates in four cases (Fig. 2; Appendix I), but most of these differences were not statistically significant after Bonferroni correction. Attack rates were significantly lower on the presumed novel host *S. gigantea* at Jackson, TN (Fig. 2).

In 2001, but not in 2004, the direction and extent of EFS varied strongly and significantly among sites (Table 4, host \times site interactions). In 2004, when the lack of an interaction allowed us to interpret main effects, there was significant variation among sites in parasitoid attack, but no significant EFS on either host (Table 4B).

Two sites had data for multiple years. At Fredericton, NB, there was no significant enemy-free space in any of the 3 years surveyed, and no changes through time (Table 5A). At Lone Tree, IA, however, enemy-free space switched dramatically from host to host between 2000 (less attack on *S. altissima*) and 2001 (less attack on *S. gigantea*; significant host \times year interaction, Table 5B).

Epiblema scudderiana

For *Epiblema*, larval dissections revealed substantial numbers of internal parasites (Fig. 3). In 2004 total attack rates, including internal parasites, ranged as high as 86% (Swanton, VT, *S. altissima*). However, the total attack rate may overestimate actual mortality, since not all parasitoids detectable in dissections will develop successfully. Therefore, we also analyzed predissection data, which represent the minimum mortality rate and which also provided more power to detect variation among sites and years in parasitoid attack (since we had twice as many year \times site combinations). In predissection data, apparent attack rates

ranged from 4.6% (Toronto, ON, 2003, *S. altissima*) to 55% (Swanton, VT, 2004, *S. gigantea*). Gallmakers on *altissima* had lower predissection attack rates in four cases, and gallmakers on *gigantea* in two cases (Fig. 3; Appendix I), but most of these differences were not statistically significant after Bonferroni correction. Attack rates were significantly lower on *S. gigantea* at Milaca, MN, in 2002 and on *S. altissima* at Toronto, ON, in 2004.

In 2003, variation in EFS among (two) sites was marginally significant (Table 6A, host \times site interaction); there was significant variation in overall parasitoid attack among sites, but no overall difference in attack rate between host plants. In 2004, predissection data showed no evidence for spatial variation in EFS (three sites; Table 6B). There was again significant variation in overall parasitoid attack among sites, and this time significant overall EFS on *S. altissima* (the ancestral host; Table 6B). Postdissection data for 2004, however, showed neither a significant host \times site interaction nor a significant host effect (analysis not shown).

Two sites had predissection data for multiple years. At Toronto, there was significant enemy-free space on *S. altissima*, similarly between years even though overall attack rates increased (Table 7A, year effect, but no host \times year interaction). In contrast, at Milaca attack was overall lower on *S. gigantea*, but the attack difference shifted dramatically among years (Table 7B, significant host \times year interaction).

Discussion

Complex patterns in enemy-free space for goldenrod herbivores

We found no consistent pattern in parasitoid attack on any of our three gallmakers, and therefore the notion that a novel host might provide consistent EFS with respect to parasitoids is not supported by our data. For all three herbivores (and regardless of which *Solidago* species is *Epiblema*'s ancestral host), we observed parasitoid EFS on the novel host at some sites/years, but the reverse at others; even for year/site contrasts where the host providing EFS did not change, the strength of the effect often did. We emphasize that we are not merely documenting spatial and temporal variation in parasitoid attack on a single herbivore—such variation is expected and has been amply documented (e.g., Feeny et al. 1985; Mira and Bernays 2002; Stireman and Singer 2002; Singer and Stireman 2003; Kumpulainen et al. 2004; Singer et al. 2004).

Instead, what we describe is variation in the *relative* attack rate on the two herbivore host forms where they occur in sympatry. Dramatic variation in enemy-free space for our herbivores was even apparent among neighboring sites: in 1993 across three Vermont sites just 30 km apart *Eurosta* attack ranged from (nonsignificantly) higher on *S. gigantea* to eightfold higher on *S. altissima* (Fig. 1).

Even a strong biogeographic pattern in the occurrence of a major *Eurosta* parasitoid did not swamp out finer-scale variation in relative attack on that gallmaker. *Eurytoma obtusiventris* is a common parasitoid in eastern collections, where it attacks *Eurosta* galls on *S. altissima* almost exclusively, contributing to high mortality rates on *S. altissima*. As a result, *E. obtusiventris* provides enemy-free space on *S. gigantea* at sites where it is abundant (Brown et al. 1995). *E. obtusiventris* is rare to absent at midwestern sites (e.g., Ames, IA, and Saint Paul, MN), where other parasitoids attack without providing EFS on *S. gigantea*. However, even within the range of *E. obtusiventris*, we see sites that resemble midwestern sites in their lack of EFS (e.g., Ascutney and Swanton, VT; Fig. 1). Variation in EFS within the range of *E. obtusiventris* may arise in part because that species' thelytokous life history allows rapid and severe population fluctuations.

Temporal variation in enemy-free space, even at single sites, was as strong as spatial variation with years, at least for *Epiblema* and *Gnorimoschema* (for *Eurosta*, the only site with multiple years' data did not show a shift in EFS). For *Epiblema* at Milaca, MN, attack shifted from eightfold higher on *S. altissima* in 2002 to 40% higher in 2003 and to (nonsignificantly) lower in 2004 (Fig. 3; predissection data). For *Gnorimoschema* at Lone Tree, IA, the temporal shift was even more striking, with a reversal of enemy-free space in consecutive years: gallmakers on *S. gigantea* experienced about 50% more attack in 2000, but 40% less attack in 2001.

Of course, because we focused on parasitoid attack, we cannot exclude the possibility that some other, unmeasured source of mortality (for instance, bird predation or fungal disease) provides consistent EFS for our goldenrod herbivores even though parasitoids do not. However, at least for *Eurosta* and *Gnorimoschema*, we consider this unlikely. For *Eurosta*, bird predation can equal or exceed parasitoid attack; however, available data suggest that the direction of bird EFS differs among sites and/or years just as we found for parasitoid EFS (higher attack on *S. altissima* in New England, Brown et al. 1995; but higher attack on *S. gigantea* in Minnesota, Poff et al. 2002). For

Gnorimoschema, predation (by birds, mammals, or invertebrate predators) is very rare, and losses to unexplained mortality (which would include disease) are small compared with losses to parasitoid attack. Bird attack on *Epiblema* is common, but we lack the data necessary to assess patterns in bird attack between goldenrod species.

One of our aims was to compare estimates of EFS for a host generalist (*Epiblema*), a recent pair of host races (*Eurosta*), and an older cryptic-species pair (*Gnorimoschema*). This comparison is of particular interest because if EFS results mainly from an evolutionary lag in parasitoid search behavior or exploitation ability, then it ought to be a transient phase in the process of host shifting. Our data provide no evidence of this, largely because even the recent host-race pair did not show a consistent pattern in EFS. Of course, it is possible that typical parasitoid lags are shorter than the age of the *Eurosta* host-race pair; however, even experimental transplants that simulate brand-new host shifts do not necessarily show consistent EFS (Gratton and Welter 1999). On the other hand, if one host plant were intrinsically inhospitable to (all) parasitoid activity, we would have expected consistent EFS on the same host for all three herbivores (e.g., Le Corff et al. 2000; Barbosa et al. 2001); we did not see this pattern either.

How typical are our goldenrod results?

We do not know whether our results are typical of herbivores showing recent host shifts, because there are so few spatially and/or temporally extensive studies with which to compare (Table 1A). Other studies have found variation in EFS in space, and the only studies demonstrating temporally consistent EFS were short-term (2–4 years) and considered just a single site. Of course, there may be herbivores for which EFS is strong and consistent on novel hosts—but there are none yet for which such consistency has been demonstrated for more than a few sites or years (Table 1). Our data show some of the strongest variation in EFS yet reported, both in time and in space, although this may be only because our study had a larger temporal and especially spatial extent than any other. The variation shown in the literature (Table 1) supports the view that temporal and spatial variation in EFS is likely to be common if not universal. As a result, ecologists should think about enemy-free space as part of the emerging paradigm of ecological and evolutionary forces as a temporal and geographic mosaic (Thompson 1994, 1997; Schiers and De Bruyn 2002; Forde et al. 2004).

Implications for models of host shifting

What do our results have to say about the conceptual models of herbivore host shifts that sparked our interest in enemy-free space? Our data, along with our survey of the literature (Table 1), are very clear: making a host shift does not automatically lead to consistent EFS. The simplest conceptual models of EFS in host shifts, then, are firmly rejected.

We cannot, however, rule out a more complex role for EFS in the host-shifting process. We can take two slightly different perspectives on this complexity. First, we might ask how and at what scales the EFS mosaic across time and space is integrated in a net selective force on incipient host races—perhaps even easing host shifting overall despite opposing it at some places and times. Attack rates in allopatric populations of host-plant pairs, not just the sympatric populations considered here, would be relevant to such an integration (e.g., Brown et al. 1995). Alternatively, we could imagine EFS as a window of opportunity that opens and closes in space and time. Successful host shifting, then, might depend on a time and place where the EFS window opens far enough and long enough—for instance, where and when the novel host happens to provide EFS for many consecutive years. Such window-opening events might be uncommon on ecological time scales, and therefore rarely observed, and yet happen often enough on evolutionary time scales to permit the kind of frequent host shifting that we infer from phylogenetic and other evidence. It will be difficult to resolve these issues without much more data for many more herbivores, and without repeated measurement of enemy attack on herbivores across many years and many sites. The consequences of spatially and temporally dynamic EFS, as well as the potential interplay of EFS with physiological, phenological, and competitive consequences of the use of a novel host, deserve detailed theoretical exploration.

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