

Is it enemy-free space? The evidence for terrestrial insects and freshwater arthropods

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Abstract. 1. Enemy-free space (EFS) was defined by Jeffries & Lawton (1984) as 'ways of living that reduce or eliminate a species' vulnerability to one or more species of natural enemies'. EFS has emerged in the literature as a significant niche-moulding factor. However, the lack of consistency among the empirical studies as to how EFS should be defined, and what hypotheses should be tested in order to evaluate its relative importance, prompted us to review the literature and to propose a working definition that results in a general set of testable hypotheses.

2. To test the relative importance of EFS in structuring the communities of organisms, we propose a set of three falsifiable null hypotheses that must be tested sequentially and rejected. Ho1: The fitness of the organism in an original habit (e.g. on an original host plant) in the presence of natural enemies is equal to the fitness of the organism in that habit in the absence of natural enemies. Acceptance of the alternative hypothesis that the fitness of the organism in the presence of natural enemies is less than in the absence of natural enemies is necessary to demonstrate the importance of natural enemies. Ho2: The fitness of the organism in an alternative habit with natural enemies is equal to the fitness of the organism in the original habit with natural enemies. Acceptance of the alternative hypothesis that the fitness of the organism in the alternative habit with natural enemies is greater than that in the original habit with natural enemies is necessary to demonstrate that the alternative habit provides EFS. Ho3: The fitness of the organism in an alternative habit without natural enemies equals the fitness of the organism in the original habit without natural enemies. Acceptance of the alternative hypothesis that the fitness of the organism in an alternative habit without natural enemies is less than in the original habit without natural enemies is necessary to demonstrate the relative importance of EFS compared with other co-occurring niche-moulding factors such as competition or host nutritional quality.

3. We searched the literature and evaluated fifty-three references (nineteen references to seventeen different terrestrial systems and thirty-four references to twenty-four different freshwater systems) to test our hypotheses.

4. Of the forty-one systems examined, nineteen (46%) tested only for differences in vulnerability of the prey or host species between EFS and non-EFS options (our Ho2); sixteen (39%) tested for the importance of natural enemies and the effectiveness of the alternative habit in providing EFS (our Ho1 and Ho2); and only ten systems (24%) tested for Ho1, Ho2 and the relative importance of EFS in the system as measured by fitness (our Ho3).

5. Of the systems that tested for EFS, sixteen of nineteen (84%), thirteen of sixteen (81%) and seven of ten (70%) showed evidence in support of the existence of EFS according to hypothesis Ho2 only, hypotheses Ho1 and Ho2, and our three working hypotheses, respectively.

6. These results indicate that very few studies have actually tested for the existence of EFS. Nevertheless, results from this limited number of natural systems suggest that EFS may be important in moulding the niches of arthropods. Because of the large number of claims for EFS in systems where none of the basic hypotheses were investigated, we suggest that authors test for EFS experimentally, be judicious in selecting articles to cite in support of EFS, and exert care in attributing it as a selective force in the evolution of arthropods in specific systems.

Key words. Enemy-free space, natural enemies, niche, community structure.

Introduction

Enemy-free space (EFS) was defined by Jeffries & Lawton (1984) as 'ways of living that reduce or eliminate a species' vulnerability to one or more species of natural enemies'. Over the last decade this paradigm has emerged as a significant mechanism hypothetically responsible for the partitioning of the environment among species of herbivorous insects (Brower, 1958; Gilbert & Singer, 1975; Smiley, 1978; Price *et al.*, 1980; Atsatt, 1981b; Lawton, 1978; Lawton & Strong, 1981; Jeffries & Lawton, 1984; Lawton, 1986a, b; Bernays & Graham, 1988; Holt & Lawton, 1993, 1994).

The concept of EFS has been observed for more than 2000 years (Fryer, 1986) with Lawton (1978, 1986a), Lawton & Strong (1981) and Jeffries & Lawton (1984) (herein J & L) summarizing the available information and explicitly formulating a hypothesis that niche differences between herbivorous species are driven by competition for EFS. In their review on the subject, J & L emphasized that competition for EFS among herbivores, along with the effects of other factors such as the physical environment, the nature and rate of supply of food, and interspecific competition for other limiting resources, are important variables influencing species' niches. On the other hand, the evidence on EFS compiled by J & L fails to test the hypothesis that niche differences between species are driven by competition for EFS. Furthermore, J & L's criterion for the existence of EFS in a system is limited to documenting differential survival between the potential habits of an organism and in the presence of natural enemies without evaluating which factors are responsible for the survival difference. This criterion resulted in the inability to distinguish EFS from other non-mutually exclusive niche-moulding forces. The importance of this limitation is that in order to understand what regulates a species' niche, we not only need to assess the importance of the individual factors (e.g. EFS) influencing herbivore fitness, but also document the comparative importance of each factor in niche regulation (Bernays & Graham, 1988).

An examination of the literature reporting support or cited in support of EFS reveals a distressing absence of coherent experimental evidence regarding the relevance of EFS for freshwater arthropods and terrestrial insect herbivores. For example, some studies that directly report the existence of EFS, or that have been cited as examples of EFS, actually suggested the existence of competitive release (Brooks & Dodson, 1965; Porter, 1973; Galbraith, 1967; Giguere, 1979; Lynch, 1979). Others failed to test for differences in vulnerability to natural enemies (Reif & Tappa, 1966; Green, 1967; Stein & Magnuson, 1976; Smiley,

1978; Heinrich, 1979; Johnson & Crowley, 1980; Opler, 1981; Hildrew & Townsend, 1982; Heads & Lawton, 1984; Hildrew *et al.*, 1984; Heads, 1986; Lancaster *et al.*, 1988; Mauricio & Bowers, 1990; Johnson & Siemens, 1991b; Fox & Eisenbach, 1992; Redfern & Cameron, 1993).

These inconsistencies indicate that there is confusion in the literature as to which hypotheses actually test the existence of EFS. Ideally, one would quantify the importance of natural enemies in the system, the existence of EFS and then the relative importance of EFS in the system (Zaret, 1969, 1972a, b; Sprules, 1972; Kerfoot, 1974, 1975, 1977; Hebert & Loaring, 1980; Damman, 1987; Solbreck *et al.*, 1989; Denno *et al.*, 1990; Ohsaki & Sato, 1990, 1994; Johnson & Siemens, 1991a; Tessier & Welser, 1991). However, some studies only tested for differences in vulnerability to natural enemies between the alternative states (with or without EFS) without estimating the actual importance of the natural enemies as mortality factors (Atsatt, 1981a, b; Kerfoot, 1982). Other studies only estimated the importance of natural enemies in the system without testing for the existence of EFS (Stein & Magnuson, 1976; Hildrew & Townsend, 1982; Redfern & Cameron, 1993).

In order to rigorously test for the existence and relative importance of EFS in a system the fitness of the organism must be compared between the original and the alternative 'way of living' or habit. Therefore, we propose the following working definition for EFS: A discrete moment in evolutionary time where the fitness of the prey, under selective pressure from the natural enemy, is increased by a change in habit.* Additionally, in the absence of natural enemies, the fitness of the prey remains constant or is reduced.

Hence, if EFS has had or is having a significant impact in structuring the communities of organisms, we would predict: (1) The fitness of the organism in an original habit (e.g. on an original host plant) without natural enemies should be greater than its fitness in the presence of natural enemies. (2) When natural enemies are present the fitness of the organism in an alternative habit (e.g. a new host plant) should be greater than its fitness in the original habit. (3) In the absence of natural enemies, the fitness of the organism in an alternative habit should be lower than the fitness of the organism in the original habit. Each of these predictions can be tested with falsifiable null hypotheses (Table 1).

Falsification of the null hypotheses results in either acceptance or failure to detect EFS in the system. Alternatives A1.1, A2.1

* A change in habit can result from a change in niche and/or a physiological, morphological, or behavioural modification in an organism.

Table 1. Falsifiable and alternative hypotheses.

| Falsifiable hypotheses (Ho) | Alternative habit provides EFS | Alternative habit does not provide EFS |
|--|---|---|
| Ho1: The fitness of the organism in the original habit with natural enemies = the fitness of the organism in the original habit without natural enemies. | A1.1: The fitness of the organism in the original habit with natural enemies < the fitness of the organism in the original habit without natural enemies. | A1.2: The fitness of the organism in the original habit with natural enemies > the fitness of the organism in the original habit without natural enemies. |
| Ho2: The fitness of the organism in the alternative habit with natural enemies = the fitness of the organism in the original habit with natural enemies. | A2.1: The fitness of the organism in the alternative habit with natural enemies > the fitness of the organism in the original habit with natural enemies. | A2.2: The fitness of the organism in the alternative habit with natural enemies < the fitness of the organism in the original habit with natural enemies. |
| Ho3: The fitness of the organism in the alternative habit without natural enemies = the fitness of the organism in the original habit without natural enemies. | A3.1: The fitness of the organism in the alternative habit without natural enemies < the fitness of the organism in the original habit without natural enemies. | A3.2: The fitness of the organism in the alternative habit without natural enemies > the fitness of the organism in the original habit without natural enemies. |

and A3.1 (Table 1) imply that natural enemies are important in the system, the alternative habit of the organism provides EFS, and EFS is a relatively significant factor in the system, respectively. Alternative A1.2 or failure to reject Ho1 indicates that natural enemies are not important in the system; alternative A2.2 or failure to reject Ho2 indicates that the alternative habit of the organism fails to provide EFS, and alternative A3.2 indicates that EFS is not a relatively significant factor in the system. Finally, failure to reject Ho3 does not exclude EFS from the system but implies the existence of other niche regulating factors such as host nutritional quality or competition for resources other than EFS.

The objectives of this paper are four. First, we evaluate the pertinent literature for the existence of EFS according to the definition of J & L. Second, we evaluate the pertinent literature for the existence of EFS according to our definition with its set of falsifiable hypotheses. Third, we attempt to obtain an understanding of the importance of EFS as a niche regulating mechanism for terrestrial insects and freshwater arthropods. Fourth, we identify areas of future research necessary to document the general occurrence of EFS.

Methods

The literature was reviewed first to test for the existence of EFS according to J & L's definition that EFS reduces the vulnerability of the prey or host organism to natural enemies in the alternate habit. In order to do this, the references were evaluated for evidence of survival differences between the original and the alternate habit of an organism. Secondly, the literature was reviewed to test the three falsifiable hypotheses derived from the predictions mentioned previously (Table 1). To evaluate the literature, biological systems were grouped into two main categories, terrestrial and freshwater systems. Finally, these groups were subdivided into systems with interspecific interactions (e.g. those between two herbivorous species and their natural enemies) or intraspecific interactions (e.g. interactions between two morphs of the same species and their natural enemies) (Tables 2 and 3).

The search was done using Current Contents in the University of California's Melvyl System®, Commonwealth Agricultural

Bureaux (CAB) Abstracts, AGRICOLA, and BIOSIS data bases from 1984 to 1994. We confined our search to those references cited as examples of EFS by other authors or references explicitly presenting empirical evidence for EFS with terrestrial insects and arthropods in freshwater systems. The bibliographies in these initially located references were examined subsequently for the identification of other relevant studies. Therefore many references were included only because they have been cited as examples of EFS by other authors.

In order to understand the regulatory effect of natural enemies and ascertain the existence of EFS in natural systems, we chose to ignore the biological control literature (with the exception of those references that mentioned EFS as an important mechanism in their systems, e.g. Ohsaki & Sato (1990, 1994) and Fox & Eisenbach (1992)) which is based in large part on artificial systems that do not provide choices between alternative habits for the prey. In total, we identified and evaluated nineteen references on seventeen different terrestrial insect systems (Table 2) and thirty-four references concerning freshwater arthropod systems (Table 3). However, five of these thirty-four references (James, 1967; Brooks, 1968; Allan, 1974; Bay, 1974; Briand & McCauley, 1979), although cited as examples of EFS, provided no experimental evidence for EFS and therefore were not included in Table 3.

Results

We point out that many of the studies in Tables 2 and 3 were not designed to test for EFS according to J & L. Similarly, none of these studies were conducted specifically to test our working hypotheses. Therefore, failure to satisfy J & L's definition of EFS and our hypotheses for verification of EFS does not reflect a lack of quality in the cited studies.

The first two falsifiable hypotheses, Ho1 and Ho2, were tested in twenty-one and nineteen of the forty-one total systems (51% and 46%), respectively. On the other hand, Ho3 was tested in only fourteen of forty-one (34%) of the systems (Table 4). This latter pattern may result from the difficulty in estimating prey fitness in the alternative habit in the absence of natural enemies. Therefore we relaxed our working definition to test only for the

Table 2. List of terrestrial systems evaluating, or cited as evaluating, enemy-free space.

| No. | Reference | System | Conclusions | Jeffries & Lawton | Hypotheses tested: outcome |
|-----|----------------------------|--|--|---|---|
| 1 | Aisalt (1981a, b)* | Type: Intraspecific. Herbivore: Lycaenid <i>Ogyris amaryllis</i> with attendant ants, <i>Iridomyrmex rufingeri</i> , and <i>Leptothorax</i> . Hosts: Several species of mistletoe (Loranthaceae). | Oviposition by <i>O. amaryllis</i> is ant-dependent. | Mistletoes with ants reduce vulnerability of <i>O. amaryllis</i> to natural enemies. | (a) Ho1 not tested. (b) Ho2: A2.1. (c) Ho3 not tested. |
| 2 | Opler (1981)† | Type: Intraspecific. Prey: The polymorphic predaceous mantispid <i>Climaciella brunnea</i> . | Frequency-dependent selection via differential predation is probably responsible for the evolution of the polymorphism and would maintain different morph frequencies at different sites. | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 3 | Heads & Lawton (1984)* | Type: Intraspecific. Host: Bracken fern (<i>Pteridium aquilinum</i>) with and without ants (<i>Myrmica scabrinodis</i> , <i>M. ruginodis</i> , and <i>Formica lemaiti</i>). Herbivores: Bracken-feeding insects. | They hypothesize that bracken herbivores have evolved and adapted to avoid ants, or fortuitously possess characteristics with the same effect. Therefore they are a special case of selection favouring evolution of prey species into enemy-free space. | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 4 | Damman (1987)† | Type: Intraspecific. Herbivore: The pyralid <i>Omphalocera munroei</i> . Hosts: Pawpaw (<i>Asimina</i> spp.) | <i>O. munroei</i> escapes predators by feeding gregariously on old, lower quality leaves, which enable them to construct better shelters. | Older leaves reduce the vulnerability of <i>O. munroei</i> to natural enemies. | (a) Ho1: A1.1. Natural enemies cause 40% mortality. (b) Ho2: A2.1. (c) Ho3: A3.1. Survival on old leaves = survival on young leaves, developmental time on old leaves > developmental time on young leaves. |
| 5 | Solbreck et al. (1989)* | Type: Intraspecific. Prey: Two (a smaller Sicilian and a larger Northern Italian) populations of the lygaeid bug <i>Lygaeus equestris</i> . Predator: Tachinid parasitoids. | The smaller body size in the Sicilian population seems to be the result of higher enemy pressure. | Adults and eggs of the smaller Sicilian population are less vulnerable to the tachinid parasitoid than the larger North Italian population. | (a) Ho1: A1.1. <i>L. equestris</i> adults suffer ≈65–75% mortality by tachinids. (b) Ho2: A2.1. (c) Ho3: A3.1. Adult <i>L. equestris</i> from the North Italian populations have higher fecundity than individuals from the Sicilian populations. Larvae emerging from larger eggs (North Italian populations) have higher survival rates than larvae from smaller eggs (Sicilian populations). |
| 6 | Johnson & Siemens (1991a)* | Type: Intraspecific. Herbivore: The bruchid beetle <i>Stator vachelliae</i> . Hosts: <i>Acacia flexuosa</i> and the non-host <i>Parkinsonia aculeata</i> . | <i>P. aculeata</i> provides EFS to <i>S. vachelliae</i> ; however, other factors prevent the complete shift to <i>P. aculeata</i> . | <i>S. vachelliae</i> is less vulnerable to egg parasitoids on the non-host <i>P. aculeata</i> than on the host <i>A. flexuosa</i> . | (a) Ho1: A1.1. Egg parasitoids cause 24% mortality on <i>A. flexuosa</i> . (b) Ho2: A2.1. (c) Ho3: A3.1. Survival of unparasitized larvae on <i>A. flexuosa</i> > survival of larvae on <i>P. aculeata</i> . |

Table 2. (Continued)

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|----|----------------------------------|---|--|--|--|
| 7 | Johnson & Siemsen (1991b)* | Type: Intraspecific Herbivore: The bruchid beetle <i>Acanthoscelides simensi</i> . Hosts: <i>Duranta dombeayana</i> (Verbenaceae). Natural enemies: Braconid wasps as predators. | Low parasitism on <i>D. dombeayana</i> is probably another factor that allowed the use of this host (enemy-free space). | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 8 | Fox & Eisenbach (1992)* | Type: Intraspecific. Herbivore: <i>Plutella xylostella</i> . Hosts: The wild species <i>Brassica nigra</i> , <i>Cardamine integrifolia</i> and <i>Erysimum cheiranthoides</i> and two crop varieties of <i>Brassica oleracea</i> , collards and red cabbage. Natural enemies: The ichneumonid wasp, <i>Diadegma insulare</i> . | Strong selection by parasitoids in agricultural systems influenced the ovipositional preferences of <i>P. xylostella</i> in low fertilized crops. This results in EFS due to the ovipositional preference for high levels of fertilization by <i>D. insulare</i> . | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3: A3.1. Survival on collards with high levels of fertilization = survival on collards with low levels of fertilization, female weight on collards with high levels of fertilization > female weight on collards with low levels of fertilization. |
| 9 | Volk (1992)* | Type: Intraspecific. Host plants: <i>Evonymus europaeus</i> and <i>Cirsium arvense</i> . Host: Bean aphid, <i>Aphis fabae</i> , attended by honeydew-collecting ants. Parasitoids: <i>Trioxys angelicae</i> , and <i>Lysiphlebus cardui</i> . | The ability of the primary parasitoid <i>L. cardui</i> to coexist with honeydew-collecting ants enables it to obtain enemy-free space from hyperparasitoids. | Ant associated <i>L. cardui</i> is less vulnerable to hyperparasitoids. | (a) Ho1: A1.1. There is a 10–60% hyperparasitism of <i>L. cardui</i> or <i>T. angelicae</i> . (b) Ho2: A2.1. The parasitoid suffered an average rate of hyperparasitism of 70% and 17% in unattended and ant-attended colonies, respectively. (c) Ho3 not tested. |
| 10 | Letourneau <i>et al.</i> (1993)* | Type: Intraspecific. Host: The euphorb <i>Endospermum labios</i> . Herbivore: <i>Lysia patroclus</i> (Uranidae). Natural enemy: The ant <i>Comptonotus quadriceps</i> . | <i>C. quadriceps</i> , which is commonly found on glabrous <i>E. labios</i> , protects the host from herbivory by <i>L. patroclus</i> . | Trees with ants are less vulnerable to herbivory from <i>L. patroclus</i> than trees without ants. | (a) Ho1: A1.1. Caterpillars can cause up to 24–38% herbivory in hosts without <i>C. quadriceps</i> . (b) Ho2: A2.1. Trees with ants suffer 13.5% herbivory compared to ≈30% suffered by trees without ants. (c) Ho3 not tested. |
| 11 | Redfern & Caméron (1993)* | Type: Intraspecific. Prey: Two coexisting types of galls (1- and 2-year galls) caused by the yew gall midge <i>Taxomyia taxi</i> . Predator: The specialist <i>Torymus nigritarsus</i> and the generalist <i>Mesopolobus diffinis</i> . | Gall size provides enemy-free space for both parasitoids, this effect contributes to the stability in the system. | Not tested. | (a) Ho1: A1.1. One-year galls frequently suffer 80% mortality by <i>M. diffinis</i> while 2-year galls suffer <40% (b) Ho2 not tested. (c) Ho3 not tested. |

Table 2. (Continued)

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| 12 | Smiley (1978) [†] | Type: Interspecific. Herbivores: <i>Heliconius melpomene</i> , <i>H. erato</i> and <i>H. cydno</i> . Hosts: <i>Passiflora</i> spp. | Host plant specific predation from ants and parasitoids may be responsible for host specificity of <i>H. melpomene</i> on <i>P. foerstedii</i> . | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 (failure to reject). In the absence of natural enemies, growth rate of <i>H. melpomene</i> was similar on all hosts. |
| 13 | Heinrich (1979) [†] | Type: Interspecific. Herbivore: Caterpillars. Natural enemies: Birds. | Bird predation selected for differences in coloration and behaviour in caterpillars. | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 14 | Gross & Price (1988) [*] | Type: Interspecific. Herbivore: The leafminers <i>Tildenia inconspicua</i> and <i>T. georgei</i> . Hosts: Horseneettle, <i>Solanum carolinense</i> , and groundcherry, <i>Physalis heterophylla</i> var. <i>ambigua</i> . Natural enemies: six braconid, two eulophid, and one eulophid species. | <i>T. inconspicua</i> developed endophytic behaviour as an adaptation to stellate trichomes. As a result it uses 'enemy-rich space'. | The endophytic <i>T. inconspicua</i> is more vulnerable to natural enemies than the exophytic <i>T. georgei</i> . | (a) Ho1: A1.1. Natural enemies cause 33.7% mortality. (b) Ho2: A2.2. (c) Ho3 not tested. |
| 15 | Mauricio & Bowers (1990) [†] | Type: Interspecific. Herbivore: The cryptic butterfly <i>Pieris rapae</i> on its host <i>Brassicaceae oleraceae</i> var. <i>botrytis</i> and <i>Raphanus sativus</i> and the aposomatic <i>Euphydryas phaeton</i> on its host <i>Chelone glabra</i> . | Predator avoidance does not influence the foraging behaviour of <i>Pieris rapae</i> . | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 16 | Denno et al. (1990) [*] | Type: Interspecific. Herbivore: The leaf beetles <i>Pharora vitellinae</i> and <i>Galerucella lineola</i> . Hosts: Willow species with varying levels of salicylates. <i>Salix dasycadlos</i> , <i>S. fragilis</i> and <i>S. viminalis</i> . Natural enemy: The coccinellid <i>Adalia bipunctata</i> . | <i>P. vitellinae</i> larvae sequesters salicylates and other phenolic glycosides from <i>S. fragilis</i> to produce defensive secretions. Hence, <i>S. fragilis</i> provides EFS to <i>P. vitellinae</i> . | <i>P. vitellinae</i> larvae on <i>S. fragilis</i> is less vulnerable to the coccinellid <i>A. bipunctata</i> than <i>P. vitellinae</i> larvae on non-salicylate producing willows such as <i>S. viminalis</i> . | (a) Ho1: A1.1. <i>A. bipunctata</i> causes 97–100% mortality. (b) Ho2: A2.1. (c) Ho3: A3.2. Developmental time on <i>S. fragilis</i> = developmental time on <i>S. viminalis</i> , survival on <i>S. fragilis</i> > survival on <i>S. viminalis</i> , pupal weight on <i>S. fragilis</i> > pupal weight on <i>S. viminalis</i> . |
| 17 | Ohsaki & Sato (1990, 1994) [†] | Type: Interspecific. Herbivores: <i>Pieris rapae crucivora</i> , <i>P. melete</i> and <i>P. napi japonica</i> . Hosts: Ten species of wild and cultivated Crucifers. Natural enemies: The braconid <i>Cotesia glomerata</i> and the tachinid <i>Epicmopora succincta</i> . | <i>P. rapae</i> escapes <i>C. glomerata</i> and <i>E. succincta</i> by utilizing less apparent unstable environments. <i>P. melete</i> has a broader host range due to the encapsulation of <i>C. glomerata</i> eggs. <i>P. napi</i> uses the concealed host <i>Arabis</i> spp. as a refuge from natural enemies. | <i>P. napi</i> is less vulnerable to natural enemies on its normally concealed host <i>Arabis</i> spp. than on exposed crucifers, including exposed <i>Arabis</i> spp. | (a) Ho1: A1.1. <i>C. glomerata</i> and <i>E. succincta</i> cause up to 95% mortality on exposed <i>Arabis</i> spp. (b) Ho2: A2.1. (c) Ho3: A3.1. Survival on <i>Arabis</i> spp. = survival on other crucifers; pupal weight on <i>Arabis</i> spp. < pupal weight on other crucifers and developmental time on <i>Arabis</i> spp. > developmental time on other crucifers. |

* Indicates that EFS was reported or postulated as being an important factor in the system by the author(s).

Table 3. List of systems with arthropods in freshwater habitats evaluating, or cited as evaluating, enemy-free space.

| No. | Reference | System | Conclusions | Jeffries & Lawton | Hypotheses tested: outcome |
|-----|---|---|--|---|--|
| 18 | Gilbert (1967) ¹ | Type: Intraspecific. Prey: The rotifer <i>Brachionus calyciflorus</i> . Predator: <i>Asplanchna girodi</i> and <i>A.sieboldi</i> . | Selective predation by <i>A.girodi</i> and <i>A.sieboldi</i> : select for the predominance of forms of <i>B.calyciflorus</i> with long postero-lateral spines. | Spined individuals of <i>B.calyciflorus</i> are less vulnerable to predation by <i>A.girodi</i> and <i>A.sieboldi</i> . | (a) Ho1: A1.1. Adult <i>A.girodi</i> and <i>A.sieboldi</i> killed 25% and 89% of the spineless newly hatched <i>B.calyciflorus</i> , respectively. Adult <i>A.sieboldi</i> killed 100% of spineless adult <i>B.calyciflorus</i> . (b) Ho2: A2.1. Adult <i>A.girodi</i> and <i>A.sieboldi</i> killed 0% and 14% of the spined newly hatched <i>B.calyciflorus</i> , respectively. Adult <i>A.sieboldi</i> captured 78% of spineless adult <i>B.calyciflorus</i> . (c) Ho3 not tested. Temperature and nutrition have been associated with the occurrence of spined forms of <i>B.calyciflorus</i> . |
| 19 | Green (1967) ¹ | Type: Intraspecific. Prey: Polymorphic <i>Daphnia lumholzi</i> . Predator: The visually selective fish <i>Alestes baremose</i> . | The smaller forms are at an advantage in the presence of visually selective fish. | Not tested. Correlative evidence only. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 20 | Zaret (1969, 1972a, b) ¹ | Type: Intraspecific Prey: The cladoceran <i>Ceriodaphnia cornuta</i> . Predator: The fish <i>Melaniris chagresi</i> . | Variable visibility to <i>M.chagresi</i> for polymorphic forms of <i>C.cornuta</i> causes selective predation for forms lacking horns with large pigmented eyes and predominance of the horned form under such selection. | Horned forms with smaller pigmented eyes are less vulnerable to predation. | (a) Ho1: A1.1. (b) Ho2: A2.1. Laboratory choice experiments showed a significant preference for unhorned forms. (c) Ho3: A3.1. Unhorned forms have a 2.8–5.8-fold higher intrinsic rate of increase than horned forms. |
| 21 | Sprules (1972) ¹ | Type: Intraspecific. Prey: Zooplankton (<i>Diaptomus shoshone</i>). Predators: <i>Chaoborus</i> sp. (Culicidae). | <i>D.shoshone</i> is restricted to shallow ponds, where <i>Chaoborus</i> spp. do not occur, due to size-selective predation by <i>Chaoborus</i> sp. larvae in deep ponds. | <i>D.shoshone</i> is less vulnerable to <i>Chaoborus</i> spp. in shallow ponds. | (a) Ho1: A1.1. <i>Chaoborus</i> spp. can cause ≈84–90% mortality of <i>D.shoshone</i> . (b) Ho2: A2.1. (c) Ho3 (failure to reject). Survival and population numbers of <i>D.shoshone</i> in shallow and deep ponds are not significantly different. |
| 22 | Kerfoot (1974, 1975, 1977) ¹ | Type: Intraspecific. Prey: Polymorphic forms (long- and short-featured forms) of the cladoceran <i>Bosmina longirostris</i> . Predator: Visually selective fish and predatory copepods. | Heavy fish predation selects against long-featured forms during the summer and in inshore areas. Copepod predation selects against short-featured forms during winter and in offshore areas. When copepod selection relaxes short-featured forms are replaced rapidly by larger lines due to higher competitive abilities. | Long-featured forms are less vulnerable to capture by predatory copepods. Short-featured forms are less vulnerable to fish predation. | (a) Ho1: A1.1. Predatory copepods are capable of causing a 20% mortality while fish cause ≈32%. (b) Ho2: A2.1. Laboratory choice tests showed a significant preference for short-featured forms by predatory copepods. (c) Ho3: A3.1. The intrinsic rate of increase of short- and long-featured forms had a mean of 2.1 ± 0.04 and 0.11 ± 0.04 , respectively. |

Table 3. (Continued)

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|----|--------------------------------------|--|---|---|--|
| 23 | Stein & Magnuson (1976) ¹ | Type: Intraspecific. Prey: Crayfish, <i>Orconectes propinquus</i> . Predator: The smallmouth bass, <i>Micropterus dolomieu</i> . | Young crayfish are more vulnerable to predation by <i>M. dolomieu</i> than adults. Hence, young individuals significantly reduce their overall activity to escape predation. | Not tested. The effect of reducing the overall activity on vulnerability was not tested. | (a) Ho1: A1.1. Instantaneous mortality of young and old crayfish by <i>M. dolomieu</i> was 1.03 and 0.4 respectively. (b) Ho2 not tested. (c) Ho3 not tested. Although, in the absence of predators the increased activity results in increased food consumption. |
| 24 | Zaret & Suffern (1976) ¹ | Type: Intraspecific. Prey: Migrating (<i>Diaptomus gatunensis</i>) and non-migrating zooplankton. Predator: Visually selective fish (<i>Metaniris chagressi</i>). | Vertical migration by zooplankton will occur when prey populations are under intense selective pressure from predators. | Vertical migration by <i>D. gatunensis</i> reduces its vulnerability to <i>M. chagressi</i> . | (a) Ho1: A1.1. <i>M. chagressi</i> can eat up to 22% of the available <i>D. gatunensis</i> . (b) Ho2: A2.1. <i>M. chagressi</i> ate 22% and 6% of the available non-migrating and migrating <i>D. gatunensis</i> , respectively. (c) Ho3 not tested. |
| 25 | Hebert & Loaring (1980) ¹ | Type: Intraspecific. Prey: Two morphs of <i>Daphnia middendorffiana</i> (morph A with a brown dorsal carapace and long tail spine and B with a black dorsal carapace and short tail spine), <i>D. magna</i> and <i>D. pulex</i> . Predator: The copepod (<i>Heterocope septentrionalis</i>). | <i>H. septentrionalis</i> feeds selectively on morph B of <i>D. middendorffiana</i> , <i>D. magna</i> , and <i>D. pulex</i> and thus provides a possible explanation for their exclusion from habitats containing the predator. | Morph A is less vulnerable than morph B and <i>D. magna</i> , and <i>D. pulex</i> to predation by <i>H. septentrionalis</i> . | (a) Ho1: A1.1. Morph B, <i>D. magna</i> , and <i>D. pulex</i> suffer mortalities above seven individuals per predator. (b) Ho2: A2.1. Morph A suffered mortality levels under two individuals per <i>H. septentrionalis</i> . (c) Ho3: A3.1. Preliminary work indicated that morph A has a lower intrinsic rate of increase than the vulnerable <i>D. magna</i> , and <i>D. pulex</i> and morph B. |
| 26 | Sih (1980, 1982a, b) ¹ | Type: Intraspecific. Prey: Young <i>Notonecta hoffmanni</i> . Predators: Adult <i>N. hoffmanni</i> . | Juvenile <i>N. hoffmanni</i> appear capable of balancing the conflicting demands of feeding efficiently and avoiding predators. | There was no significant difference in vulnerability of juveniles of <i>N. hoffmanni</i> to <i>N. hoffmanni</i> adults between low and high predator density areas. | (a) Ho1: A1.1. Mortality caused by adult <i>N. hoffmanni</i> was 60% for first, 52% for second, and 40% for third instars. (b) Ho2 (failure to reject). (c) Ho3 not tested. An increase in feeding rate was related to an increase in time spent in a low predator density area. However, there is no relationship between feeding rate and fitness for first-instar <i>N. hoffmanni</i> . |
| 27 | Lancaster et al. (1988) ¹ | Type: Intraspecific. Prey: Caddisfly larvae, <i>Plectrocnemia conspersa</i> . Predators: Brown trout, <i>Salmo trutta</i> . | Fallen leaves in autumn provide refugia from fish. | Not tested. | (a) Ho1: A1.1. (b) Ho2 not tested. (c) Ho3 not tested. |
| 28 | Brooks & Dodson (1965) ¹ | Type: Interspecific. Prey: Small (<i>Bosmina longirostris</i> and <i>Ceriodaphnia lacustris</i>) and large (<i>Daphnia</i> spp., <i>Diaptomus</i> spp., <i>Mesocyclops edax</i> , and <i>Cyclops bicuspidatus thomasi</i>) zooplankton. Predator: The fish <i>Alosa pseudoharengus</i> . | <i>Alosa</i> spp. eliminated those zooplankters with size above 1 mm allowing the dominance of small organisms, which otherwise exist in low densities. | Competitive release. Small organisms are less vulnerable to <i>Alosa</i> spp. than large sized zooplankters. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |

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| 29 | Reif & Tappa (1966) [†] | Type: Interspecific. Prey: The cladocerans <i>Daphnia pulex</i> , <i>Daphnia dubia</i> and <i>Leptodora kindtii</i> . Predator: Smelt (<i>Osmerus mordax</i>). | The differential predation of an introduced fish (smelt) has favoured the survival of a species whose individuals are smaller (<i>D. dubia</i>) than those of the eradicated species (<i>D. pulex</i>). The larger <i>D. pulex</i> (≈ 1.3 mm) is replaced by the smaller Daphnids <i>D. galeata mendotae</i> , and <i>D. retrocurva</i> (≈ 0.8 mm) as a result of selective predation on the larger species by <i>S. gairdneri</i> . | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 30 | Galbraith (1967) [†] | Type: Interspecific. Prey: Zooplankton (<i>Daphnia pulex</i> , <i>D. galeata mendotae</i> and <i>D. retrocurva</i>). Predator: Rainbow trout (<i>Salmo gairdneri</i>). | The gelatinous green algae (undigestible to zooplankton due to physiological adaptations) are spared from grazers and can increase in number whereas smaller competitors are suppressed and larger, slower reproducing species cannot respond rapidly. | Competitive release. <i>D. galeata mendotae</i> , and <i>D. retrocurva</i> are less vulnerable to <i>S. gairdneri</i> than <i>D. pulex</i> . | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 31 | Porter (1973) [†] | Type: Interspecific. Prey: Phytoplankton. Predators: Zooplankton. | The gelatinous green algae (undigestible to zooplankton due to physiological adaptations) are spared from grazers and can increase in number whereas smaller competitors are suppressed and larger, slower reproducing species cannot respond rapidly. | Competitive release. Gelatinous green algae are less vulnerable to grazers than smaller algae. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 32 | Giguere (1979) [†] | Type: Interspecific. Prey: Small (<i>Diaphanosoma</i> spp.), mid-size (<i>Holopedium</i> spp.) and large (<i>Daphnia</i> spp.) cladocerans. Predators: The salamander <i>Ambystoma tigrinum</i> , the larval midge <i>Chaoborus americanus</i> and the copepod <i>Diaptomus shoshone</i> . | <i>Daphnia</i> becomes the dominant species in the absence of size selective predators (salamanders) due to higher competitive ability. When the salamanders are present small cladocerans become the dominant species. | Competitive release. Smaller cladocerans are less vulnerable to <i>A. tigrinum</i> . | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 33 | Lynch (1979) [†] | Type: Interspecific. Prey: The predator <i>Chaoborus americanus</i> and the cladocerans <i>Daphnia pulex</i> and <i>Ceriodaphnia reticulata</i> . Primary predator: Fish. Secondary predator: <i>Chaoborus americanus</i> . | The most abundant herbivore in the absence of vertebrate predators is <i>D. pulex</i> or <i>C. reticulata</i> . When the predator <i>C. americanus</i> is absent, <i>C. reticulata</i> is able to express its competitive superiority over <i>D. pulex</i> and becomes the dominant herbivore. | Competitive release. The larger <i>D. pulex</i> is less vulnerable to predation by <i>C. americanus</i> than the smaller <i>C. reticulata</i> . | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 34 | Johnson & Crowley (1980) [†] | Type: Interspecific. Prey: Odonate nymph spp. Predators: Different fish spp. | Differences in odonate assemblages between a predator-free pond and a lake with fish are attributed to the absence of predators in the pond which permits the more active odonate species to eliminate by competition or predation the species that dominate the lake. | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 35 | Stich & Lampert (1981) [†] | Type: Interspecific. Prey: <i>Daphnia hyalina</i> and <i>D. galeata</i> . Predators: Whitefish (<i>Coregonus warreni</i>) and perch (<i>Perca fluviatilis</i>). | Predator avoidance is one of the most important factors in vertical migration of <i>D. hyalina</i> . | Not tested. Difference in vulnerability between <i>D. galeata</i> and <i>D. hyalina</i> was not linked to migratory differences. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3: A3.1. <i>D. galeata</i> had a higher instantaneous birth rate than <i>D. hyalina</i> . |

Table 3. (Continued)

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|----|--|---|--|--|---|
| 36 | Hildrew & Townsend (1982) [†] | Type: Interspecific. Prey: Several Chironomid spp. Predator: The caddis <i>Plectrocnemia conspersa</i> . | At certain times, consumption rates were significantly lower in the more structurally complex patches of the stream, presumably because they provided prey refuge. | Not tested. | (a) Ho1: A1.1. Daily consumption rates averaged between 0.2% and 2.8% of the prey. (b) Ho2 not tested. (c) Ho3 not tested. |
| 37 | Kerfoot (1982) [†] | Type: Interspecific. Prey: <i>Daphnia</i> spp. and phantom midges <i>Chaoborus</i> spp. Predators: The visually selective fish <i>Lepomis gibbosus</i> . | <i>Chaoborus</i> larvae are less conspicuous than the pigmented <i>Daphnia</i> . Therefore predators might prey upon the conspicuous <i>Daphnia</i> . | <i>Chaoborus</i> larvae were less vulnerable than large <i>Daphnia</i> to predation. | (a) Ho1 not tested. (b) Ho2: A2.1. Laboratory choice tests showed a significant preference for large <i>Daphnia</i> over average-sized <i>Chaoborus</i> larvae. (c) Ho3 not tested. However, the author states that pigmentation provides photoprotection from short-wavelength radiation. Therefore crypsis due to transparency confers a disadvantage to <i>Chaoborus</i> . |
| 38 | Kerfoot (1982) [†] | Type: Interspecific. Prey: Water mites. Predator: Cuppies (<i>Lebiasis reticulatus</i>). | Chemically protected red-coloured water mites are more distasteful to the predator than dull-coloured species. | Chemically protected water mites are less vulnerable to predation. | (a) Ho1 not tested. (b) Ho2: A2.1. Significant rejection by the predator occurred with a 0.5–5% and 10–50% powder extract from chemically protected and unprotected mites, respectively. (c) Ho3 not tested. |
| 39 | Hildrew et al. (1984) [†] | Type: Interspecific. Prey: Large insect predators. Predator: Fish. | There are lower densities of large insect predators with increasing pH. It is possible that the presence of fish in the less acidic sites causes the decline of the more vulnerable large species. | Not tested. | (a) Ho1 not tested. (b) Ho2 not tested. (c) Ho3 not tested. |
| 40 | Heads (1986) [†] | Type: Interspecific. Prey: Damselfly nymph <i>Ischnura elegans</i> . Predator: Female adults of <i>Notonecta glauca</i> . | <i>I. elegans</i> nymphs significantly reduced their foraging activity and feeding rates when predators were present. | Not tested. | (a) Ho1: A1.1. They cite Sih (1980, 1982a, b). (b) Ho2 not tested. (c) Ho3: A3.1. The developmental rate of the active <i>I. elegans</i> is 4–18% higher than that of individuals with reduced foraging activity. |
| 41 | Tessier & Welsler (1991) [†] | Type: Interspecific. Prey: The smaller cladoceran <i>Daphnia galeata mendotae</i> and the larger <i>D. pulicaria</i> . Predators: Several fish spp. (mainly the bluegill sunfish (<i>Lepomis macrochirus</i>)). | Lakes with a large refuge (space between the thermocline and zone of anoxia) are dominated by <i>D. pulicaria</i> ; those with small refuge size are dominated by <i>D. galeata mendotae</i> . | <i>D. pulicaria</i> is restricted to refuge areas in the hypolimnion because of its greater vulnerability to fish predators. | (a) Ho1: A1.1. (b) Ho2: A2.1. (c) Ho3: A3.1. <i>D. pulicaria</i> is a superior competitor than <i>D. galeata mendotae</i> . |

* Indicates that EFS was reported or postulated as being an important factor in the system by the author(s).

† Indicates that the study was cited by other authors as an example of EFS.

Table 4. Summarized results from Tables 2 and 3.

| System type | Systems tested | | Systems with positive results | | | |
|--|---------------------------------------|-----------------------------------|-------------------------------|-------------------------------|-------------------------------|----------------------|
| | Jeffries & Lawton | First two hypotheses | All three hypotheses | Jeffries & Lawton | First two hypotheses | All three hypotheses |
| Terrestrial and intraspecific systems (<i>n</i> = 11) | 6{55}(1, 4, 5, 6, 9, 10) ^c | 5{45}(4, 5, 6, 9, 10) | 3{27}(4, 5, 6) | 5{83}(1, 4, 5, 9, 10) | 4{80}(4, 5, 9, 10) | 2{67}(4, 5) |
| Terrestrial and interspecific systems (<i>n</i> = 6) | 3{50}(14, 16, 17) | 3{50}(14, 16, 17) | 2{33}(16, 17) | 2{67}(16, 17) | 2{67}(16, 17) | 1{50}(17) |
| Freshwater and intraspecific systems (<i>n</i> = 10) | 7{70}(18, 20, 21, 22, 24, 25, 26) | 7{70}(18, 20, 21, 22, 24, 25, 26) | 4{40}(20, 21, 22, 25) | 6{86}(18, 20, 21, 22, 24, 25) | 6{86}(18, 20, 21, 22, 24, 25) | 3{75}(20, 22, 25) |
| Freshwater and interspecific systems (<i>n</i> = 14) | 3{21}(37, 38, 41) | 1{7}(41) | 1{7}(41) | 3{100}(37, 38, 41) | 1{100}(41) | 1{100}(41) |

^a The first number for each cell is the number of systems for that particular column and system type.

^b The number in curly brackets for each cell is the percentage of systems tested from the total number of systems in that particular system type (*n*).

^c The numbers in parentheses for each cell are the system numbers from Tables 2 and 3 for that particular column and system type.

^d The number in square brackets for each cell is the percentage of systems with positive results from the number of systems tested in that particular column and system type.

importance of natural enemies in the system (Ho1) and the effectiveness of the alternative habit in producing EFS (Ho2) (Table 4).

Nine of seventeen (53%) systems with terrestrial insects tested J & L's criterion; two of these found that EFS was not important (Tables 2 and 4). The first system shows an interspecific interaction between two species of herbivorous leafminers, their host plants and their natural enemies (Gross & Price, 1988). The second is an intraspecific system resulting from the interaction of a single herbivore, *Stator vachelliae*, its host plant and its natural enemies (Johnson & Siemens, 1991a). Therefore, seven of seventeen (41%) of the terrestrial systems demonstrated the existence of EFS according to J & L. Of these seventeen terrestrial systems, eight (47%) tested hypotheses Ho1 and Ho2, but only six (35%) systems demonstrated the importance of natural enemies and the existence of an alternative habit with reduced vulnerability (Tables 2 and 4). Only five terrestrial insect systems (29%) tested all three of our falsifiable hypotheses. In the intraspecific system studied by Johnson & Siemens (1991a), an alternative host *Parkinsonia aculeata* L. (Fabaceae) provided EFS for the herbivore *Stator vachelliae* Bottimer (Coleoptera: Bruchidae); however, the authors concluded that the herbivore has remained on its original host due to the effect of mechanisms other than EFS. In the interspecific study by Denno *et al.* (1990), the relative importance of EFS could not be determined. Hence, the existence and relative importance of EFS, according to our working definition, was demonstrated in three of the seventeen (18%) terrestrial systems.

Five of the fourteen interspecific freshwater systems (Brooks & Dodson, 1965; Galbraith, 1967; Porter, 1973; Giguere, 1979; Lynch, 1979) documented greater success of an organism resulting from selective predation of a competitor. Therefore, these studies suggested competitive release (Hutchinson, 1978) rather than EFS (Table 3).

Ten of the twenty-four (42%) freshwater systems (Tables 3 and 4) tested J & L's criterion. Only one intraspecific system (Sih, 1980, 1982a, b) found no differences in prey vulnerability in the alternative habit (low and high predator density areas). Three interspecific systems (Kerfoot, 1982; Tessier & Welser, 1991) showed a direct interaction between the prey and the natural enemy (Table 3). Therefore, nine of twenty-four freshwater systems (38%) demonstrated the existence of EFS according to the J & L definition. Eight (33%) of those twenty-four systems tested hypotheses Ho1 and Ho2. One of these eight (Sih, 1980, 1982a, b) found no evidence for EFS. Consequently, seven of twenty-four (29%) of the systems obtained positive results on the importance of natural enemies and the existence of an alternative habit with reduced vulnerability. Five of the twenty-four systems (21%) tested all three of our falsifiable hypotheses. In the intraspecific system studied by Sprules (1972), no difference in fitness between the original and the alternate habit was found in the absence of natural enemies. Therefore, although EFS may still be important in Sprules' (1972) system, its relative importance cannot be determined. Hence, four out of twenty-four (17%) tested Ho3, and indicated positive evidence for the relative importance of EFS.

Table 4 shows that nineteen of the forty-one systems (46%) in Tables 2 and 3 tested J & L's criterion, sixteen (39%) tested hypotheses Ho1 and Ho2 and only ten (24%) tested all three of the

falsifiable hypotheses. Although these results indicate that there is very little empirical evidence for EFS, the proportion of systems that demonstrated EFS of those systems that actually tested for EFS shows encouraging results (Table 4). Seven of nine (78%), six of eight (75%) and three of five (60%) systems with terrestrial arthropods demonstrated the existence of EFS according to J & L, hypotheses Ho1 and Ho2, and hypotheses Ho1, Ho2, Ho3, respectively. Similarly, nine of ten (90%), seven of eight (88%) and four of five (80%) systems with freshwater arthropods obtained positive results on the existence of EFS according to J & L, hypotheses Ho1 and Ho2, and hypotheses Ho1, Ho2, Ho3, respectively.

Discussion

Forty-six percent of the systems in Tables 2 and 3, all of which reported EFS or have been cited to support the concept of EFS, actually tested experimentally for differences in vulnerability between the original and alternative state of an organism which is the minimal parameter needed to quantify the existence of EFS. Thirty-nine percent of the systems failed to test for the importance of natural enemies in the original state (Ho1) and for the existence of EFS in the system (Ho2). Finally, only 24% of the forty-one systems tested for Ho1, Ho2, and the relative importance of EFS in the system (Ho3). Therefore we could only find ten systems where EFS has been tested according to our definition (Tables 2, 3 and 4).

Jeffries & Lawton (1984) noted that: 'What is not clear is how many of the examples of enemy-free space ... are genuine cases of evolution or even of coevolution of sets of victim species with one or more enemies, and how many are fortuitously evolved characteristics selected for in other circumstances'.

This inability to distinguish EFS from other non-mutually exclusive niche-moulding forces stems from the fact that most studies where EFS has been demonstrated are limited to documenting differential survival in the presence of natural enemies between the potential habits of an organism without testing for which factors are causing this difference. Furthermore, the studies in Tables 2 and 3 are not consistent with regard to which hypotheses test the existence of EFS. Some studies test only for differences in vulnerability between the original and alternative habits, although increased survival does not necessarily mean an increase in fitness for the organism. For example, Gross & Price (1988) showed that, in the presence of natural enemies, the survival of the horsenettle leafminer, *Tildenia inconspicuella* (Murtfeldt) (Lepidoptera: Gelechiidae) (which spends its entire larval life inside a single mine, i.e. is endophytic), is lower than the survival of the groundcherry leafminer, *T.georgei* (which spends considerable time outside its mine, i.e. is exophytic). The authors speculated that since the exophytism is probably the primitive behaviour of this group of leafminers, *T.inconspicuella* most likely developed endophytism as an adaptation to the stellate trichomes present in horsenettle. Hence, if the primitive exophytic ancestors of *T.inconspicuella* suffered similar parasitism levels as the exophytic *T.georgei*, and if successful host shifts result from higher overall fitness on the new host, the fact that horsenettle leafminer was capable of adapting to a new host indicates that overall fitness in the 'alternative habit' or endophytism in

horsenettle is higher than the fitness on the 'original habit' or primitive exophytic form. Therefore, if the previously stated conditions for host shift hold true for this system, a difference in vulnerability to natural enemies between the original and alternative habits is not a good estimate for overall fitness of *T.inconspicuell*.

Only 24% of the systems in Tables 2 and 3 provided good empirical evidence on the prevalence of EFS according to our three working hypotheses; this indicates that it is difficult to evaluate the relative importance of EFS in relation to other niche-moulding factors (e.g. competition). This may be due to the fact that few natural systems allow an estimation of prey fitness within the alternative habit in the absence of natural enemies. Therefore, whenever possible, experimental manipulation of the system must be employed (Lawton, 1986a). The significance of determining the relative importance of EFS is amply illustrated in the studies by Atsatt (1981a, b), who demonstrated that the association of the nymphalid, *Ogyris amaryllis* Hewitson (Lepidoptera), with ants reduced its vulnerability to natural enemies. However, there is no information on the effect of the ants on the fitness of *O.amaryllis* in the absence of natural enemies. Consequently, the role of other effects resulting from the *O.amaryllis*-ant association cannot be excluded as possibly playing a major role eliciting this lycaenid-ant interaction. One such effect could be the existence of an increased development efficiency by *O.amaryllis* derived from its association with ants (Table 2). For example, Cushman *et al.* (1994) demonstrated that the presence of the ant, *Anonychomyrma nitidiceps* (André) (Hymenoptera: Formicidae), resulted in a 31-76% increase in larval biomass and a 37% and 69% reduction, respectively, in larval and pupal development times for the lycaenid *Paralucia aurifera* (Blanchard) (Lepidoptera). According to their estimates, these factors reduced development time by 50%.

In addition, performance parameters such as pupal weight, developmental rate, and survival are not always correlated with fitness (Thompson, 1988). Therefore an effort should be made to obtain better fitness estimates such as intrinsic rate of increase or correlations between these parameters and fecundity. In the study by Denno *et al.* (1990), larvae of *Phratora vitellinae* L. (Coleoptera: Chrysomelidae) feeding on *Salix fragilis* L. (Salicaceae) were less vulnerable to the coccinellid *Adalia bipunctata* (L.) (Coleoptera) than were *P.vitellinae* larvae on non-salicylate-producing willows such as *S.viminalis*. In the absence of natural enemies the developmental time of *P.vitellinae* on *S.fragilis* was not significantly different from its developmental time on *S.viminalis*; however, survival on *S.fragilis* was significantly greater than survival on *S.viminalis*. Finally, pupal weight on *S.fragilis* was also greater than that on *S.viminalis*. The authors recognized the differences in nutritional quality between these two willow species and suggested 'that the slight nutritional inferiority of *S.viminalis* does not appreciably influence the fitness of *P.vitellinae* and consequently is not primarily responsible for its exclusion on this host'. Nevertheless, in the absence of fecundity data, it is difficult to distinguish between host plant effects and EFS in this system.

Table 4 indicates that of the systems that actually tested for EFS, 84%, 81% and 70% showed evidence in support of the existence of EFS according to J & L's criterion, hypotheses Ho1 and Ho2 only, and all three working hypotheses, respectively,

suggesting that natural enemies may be important in niche differentiation (Lawton, 1986a). However, care must be taken when interpreting these results because the number of systems for which there is evidence on EFS is small, and because an inherent problem is that negative results are commonly not published; therefore our sample may not be a true representation of the importance of EFS in structuring arthropod communities.

The proportion of interspecific systems that tested for EFS is approximately 1 and 0.20 of terrestrial and freshwater intraspecific systems, respectively (Table 4). Furthermore, the proportion of terrestrial intraspecific systems with evidence in support of EFS was about 1.25 times that of terrestrial interspecific systems. This result may stem from the fact that the comparison of two populations of the same species with different habits is likely to highlight contemporary effects by natural enemies (EFS), whereas the comparison of different species, even closely related, may not.

Lawton (1986a) showed that natural enemies can mould many aspects of prey or host species' niches, and that factors such as location within the host, morphology, seasonal variation, host plant, and niche differences of related species feeding on the same host plant affect the vulnerability of the prey or hosts to their natural enemies. Jeffries & Lawton (1984) classified the studies on EFS under four broad mechanisms through which the impact of natural enemies was reduced; these were morphology, size, position and other mechanisms* (toxicity, speed of movement, etc.). Our analysis shows five mechanisms (changes in habits) through which prey populations obtained EFS (Tables 2 and 3). These were adaptations in morphology and size (Solbreck *et al.*, 1989; Gilbert, 1967; Kerfoot, 1974, 1975, 1977; Hebert & Loaring, 1980), position (Ohsaki & Sato, 1990, 1994; Sprules, 1972; Zaret & Suffern, 1976; Tessier & Welser, 1991), interspecific interactions (Atsatt, 1981a, b; Volkl, 1992; Letourneau *et al.*, 1993), visibility (Zaret, 1969, 1972a, b; Kerfoot, 1982) and chemistry (Kerfoot, 1982). We chose to classify morphology and size together because in many systems such as in those with zooplankton morphs (Gilbert, 1967; Kerfoot, 1974, 1975, 1977), it is difficult to separate these two characteristics since size differences result from morphological adaptations. In contrast to J & L we included visibility, chemistry and interspecific interactions categories in order to understand better what type of adaptations confer EFS to arthropods. Interestingly, studies of freshwater and interspecific terrestrial systems failed to show even a single case of EFS developing through interspecific interactions, whereas intraspecific terrestrial systems demonstrated three cases of interspecific interactions contributing to EFS according to the criterion of J & L and two cases according to hypotheses Ho1 and Ho2 (Table 4). In these three systems, ants provide EFS to an associated organism such as a lycaenid butterfly (Atsatt, 1981a, b), a hymenopteran parasitoid (Volkl, 1992) and an euphorbiaceous tree (Letourneau *et al.*, 1993). In Letourneau *et al.* (1993) there is a mutualistic interspecific interaction wherein an ant, *Camponotus quadriceps* F. (Hymenoptera: Formicidae), obtains food, whereas the plant (*Endospermum labios* Schodde) (Euphorbiaceae) obtains protection from herbivores. The studies by Atsatt (1981a, b) also show a mutualistic interaction in which ants obtain energy from a nectar secretion, while a lycaenid larva obtains EFS and maybe other benefits. The study by Volkl (1992) shows a system where *Lysiphlebus cardui* (Marshall)

(Hymenoptera: Aphididae), a specialized parasitoid of the bean aphid, *Aphis fabae cirsiacanthoides* (Scop.) (Homoptera: Aphididae) takes advantage of the protection of aphid-tending ants by avoiding their defences for oviposition but using their protection from hyperparasitoids.

Although studies of freshwater systems often include organisms feeding at various trophic levels, researchers in freshwater systems have been 1.15, 1.17 and 1.33 times more successful in finding evidence for EFS according to the J & L definition, hypotheses Ho1 and Ho2 and all three of our falsifiable hypotheses, respectively. The greater success of researchers in freshwater systems as compared with studies on terrestrial insects may be based (at the risk of sounding defensive) on the fact that freshwater systems commonly show top-down interactions and are more tractable than terrestrial systems (Strong, 1992; Wootton & Power, 1993).

Our results (Tables 2, 3 and 4) indicate that the evidence for the paradigm that EFS is an important niche moulding mechanism is very limited, with only a few studies actually testing for the existence of EFS. Nevertheless, results from this limited number of natural systems suggest that EFS may be important in moulding the niches of arthropods. The development of a reasonable body of literature that tests specifically for the effects of natural enemies (Ho1), the effectiveness of EFS (Ho2), and the relative importance of EFS, by comparing the fitness of the organism in the alternative habit and in the absence of natural enemies (Ho3), will significantly increase our understanding of the importance of EFS as a niche regulating factor. We believe that our definition addresses the problem of estimating the relative importance of EFS. Furthermore, the use of our working hypotheses should contribute to the elaboration of a consistent and reasonable body of information on the importance of EFS as a niche-moulding force. Until such a database is available, we suggest that authors test for EFS experimentally, be judicious in selecting articles to cite in support of EFS, and exert care in attributing it as a selective force in the evolution of arthropods in specific systems.

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References

- Allan, D. (1974) Balancing predation and competition in cladocerans. *Ecology*, **55**, 622–629.
- Atsatt, P.R. (1981a) Ant-dependent food plant selection by mistletoe butterfly *Agyris amaryllis* (Lycaenidae). *Oecologia*, **48**, 60–63.
- Atsatt, P.R. (1981b) Lycaenid butterflies and ants: selection for enemy-free space. *The American Naturalist*, **118**, 638–654.
- Bay, E.C. (1974) Predator–prey relationships among aquatic insects. *Annual Review of Entomology*, **19**, 441–453.
- Bernays, E.A. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology*, **69**, 886–892.
- Briand, F. & McCauley, E. (1979) Zooplankton grazing and phytoplankton species richness: field test of the predation hypothesis. *Limnology and Oceanography*, **24**, 243–252.
- Brooks, J.L. (1968) The effects of prey size selection by lake planktivores. *Systematic Zoology*, **17**, 273–291.
- Brooks, J.L. & Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28–35.
- Brower, L.P. (1958) Bird predation and foodplant specificity in closely related procyptic insects. *The American Naturalist*, **92**, 183–187.
- Cushman, J.H., Rashbrook, V.K. & Beattie, A.J. (1994) Assessing benefits to both participants in a Lycaenid–ant association. *Ecology*, **17**, 1031–1041.
- Damman, H. (1987) Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology*, **68**, 88–97.
- Denno, R.F., Larson, S. & Olmstead, K.L. (1990) Role of enemy-free space and plant quality in host plant selection by willow beetles. *Ecology*, **71**, 124–137.
- Fox, L.R. & Eisenbach, J. (1992) Contrary choices: possible exploitation of enemy-free space by herbivorous insects in cultivated vs. wild crucifers. *Oecologia*, **89**, 574–579.
- Fryer, G. (1986) Enemy-free space: a new name for an ancient ecological concept. *Biological Journal of the Linnean Society*, **27**, 287–292.
- Galbraith, M.G. (1967) Size-selective predation on *Daphnia* by rainbow trout and yellow perch. *Transactions of the American Fisheries Society*, **96**, 1–10.
- Giguere, L. (1979) An experimental test of Dodson's hypothesis that *Ambystoma* (a salamander) and *Haoborus* (a phantom midge) have complementary feeding niches. *Canadian Journal of Zoology*, **57**, 1091–1097.
- Gilbert, J.G. (1967) *Asplanchna* and postero-lateral spine production in *Brachionus calyciflorus*. *Archiv für Hydrobiologie*, **64**, 2–59.
- Gilbert, L.E. & Singer, M.C. (1975) Butterfly ecology. *Annual Review of Ecology and Systematics*, **6**, 365–397.
- Green, J. (1967) The distribution and variation of *Daphnia lumholzi* (Crustacea: Cladocera) in relation to fish predation in Lake Albert, East Africa. *Journal of Zoology*, **151**, 181–197.
- Gross, P. & Price, P.W. (1988) Plant influences on parasitism of two leafminers: a test of enemy-free space. *Ecology*, **69**, 1506–1516.
- Heads, P.A. (1986) The costs of reduced feeding due to predator avoidance: potential effects on growth and fitness in *Ischnura elegans* larvae (Odonata: Zygoptera). *Ecological Entomology*, **11**, 369–377.
- Heads, P.A. & Lawton, J.H. (1984) Bracken, ants and extrafloral nectaries. II. The effect of ants on the insect herbivores of bracken. *Journal of Animal Ecology*, **53**, 1015–1031.
- Hebert, P.D. & Loaring, J.M. (1980) Selective predation and the species composition of Arctic ponds. *Canadian Journal of Zoology*, **58**, 422–426.
- Heinrich, B. (1979) Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. *Oecologia*, **42**, 325–337.
- Hildrew, A.G. & Townsend, C.R. (1982) Predators and prey in a patchy environment: a freshwater study. *Journal of Animal Ecology*, **51**, 797–815.
- Hildrew, A.G., Townsend, C.R. & Francis, J. (1984) Community structure in some southern English streams: the influence of species interactions. *Freshwater Biology*, **14**, 297–310.
- Holt, R.D. & Lawton, J.H. (1993) Apparent competition and enemy free space in insect host-parasitoid communities. *The American Naturalist*, **142**, 623–645.
- Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495–520.
- Hutchinson, G.E. (1978) *An Introduction to Population Ecology*. Yale University Press, New Haven.

- James, H.G. (1967) Seasonal activity of mosquito predators in woodland pools in Ontario. *Mosquito News*, **27**, 453–457.
- Jeffries, M.J. & Lawton, J.H. (1984) Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.
- Johnson, C.D. & Siemans, D.H. (1991a) Expanded oviposition range by a seed beetle (Coleoptera: Bruchidae) in proximity to a normal host. *Environmental Entomology*, **20**, 1577–1582.
- Johnson, C.D. & Siemans, D.H. (1991b) Interactions between a new species of *Acanthoscelides* and a species of Verbanaceae a new host family from bruchidae (Coleoptera). *Annals of the Entomological Society of America*, **84**, 165–169.
- Johnson, D.M. & Crowley, P.H. (1980) Habitat and seasonal segregation among coexisting odonate larvae. *Odonatologica*, **9**, 297–308.
- Kerfoot, W.C. (1974) Egg-size cycle of a cladoceran. *Ecology*, **55**, 1259–1270.
- Kerfoot, W.C. (1975) The divergence of adjacent populations. *Ecology*, **56**, 1298–1313.
- Kerfoot, W.C. (1977) Competition in cladoceran communities: the cost of evolving defenses against copepod predation. *Ecology*, **58**, 303–313.
- Kerfoot, W.C. (1982) A question of taste: crypsis and warning coloration in freshwater zooplankton communities. *Ecology*, **63**, 538–554.
- Lancaster, J., Hildrew, A.G. & Townsend, C.R. (1988) Competition for space by predators in streams: field experiments on a net-spinning caddisfly. *Freshwater Biology*, **20**, 185–193.
- Lawton, J.H. (1978) Host plant influences on insect diversity; the effects of space and time. *Diversity of Insect Faunas* (ed. by L. A. Mound and N. Waloff), pp. 105–125. Blackwell Scientific Publications, Oxford.
- Lawton, J.H. (1986a) The effect of parasitoids on phytophagous insect communities. *Insect Parasitoids: 13th Symposium of the Royal Entomological Society* (ed. by J. Waage and D. Greathead), pp. 265–287. Academic Press, London.
- Lawton, J.H. (1986b) Surface availability and insect community structure: The effects of architecture and fractal dimensions of plants. *Insects and The Plant Surface* (ed. by B. Juniper and T. R. E. Southwood), pp. 317–331. Arnold, London.
- Lawton, J.H. & Strong, D.R. (1981) Community patterns and competition in folivorous insects. *The American Naturalist*, **118**, 317–338.
- Letourneau, D.K., Arias, F.G. & Jebb, M. (1993) Coping with enemy-filled space: herbivores on *Endospermum* in Papua New Guinea. *Biotropica*, **25**, 95–99.
- Lynch, M. (1979) Predation, competition and zooplankton community structure: an experimental study. *Limnology and Oceanography*, **24**, 253–272.
- Mauricio, R. & Bowers, M.D. (1990) Do caterpillars disperse their damage?: larval foraging behavior of two specialist herbivores, *Euphydryas phaeton* (Nymphalidae) and *Pieris rapae* (Pieridae). *Ecological Entomology*, **15**, 153–161.
- Ohsaki, N. & Sato, Y. (1990) Avoidance mechanisms of three *Pieris* butterfly species against the parasitoid wasp *Apanteles glomeratus*. *Ecological Entomology*, **15**, 169–176.
- Ohsaki, N. & Sato, Y. (1994) Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. *Ecology*, **75**, 59–68.
- Opiet, P.A. (1981) Polymorphic mimicry of polistine wasps by a neotropical neuropteran. *Biotropica*, **13**, 165–176.
- Porter, K.G. (1973) Selective grazing and differential digestion of algae by zooplankton. *Nature*, **20**, 170–180.
- Price, P.W., Bouton, C.E., Gross, P., McPherson, B.A., Thompson, J.N. & Weiss, A.E. (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41–65.
- Redfern, M. & Cameron, A.D. (1993) Population dynamics of the yew gall midge *Taxomyia taxi* and its chalcid parasitoids: a 24-year study. *Ecological Entomology*, **18**, 365–378.
- Reif, C. & Tappa, D.W. (1966) Selective predation: smelt and cladocerans in Harveys Lake. *Limnology and Oceanography*, **11**, 437–438.
- Sih, A. (1980) Optimal behavior: can foragers balance two conflicting demands. *Science*, **210**, 1041–1043.
- Sih, A. (1982a) Foraging strategies and the avoidance of predation by an aquatic insect *Notonecta hoffmanni*. *Ecology*, **63**, 786–796.
- Sih, A. (1982b) Optimal patch use: variation in selective pressure for efficient foraging. *The American Naturalist*, **120**, 666–685.
- Smiley, J. (1978) Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science*, **201**, 745–747.
- Solbreck, C., Olsson, R., Anderson, D.B. & Förare, J. (1989) Size, life history and responses to food shortage in two geographical strains of a seed bug *Lygaeus equestris*. *Oikos*, **55**, 387–396.
- Sprules, W.G. (1972) Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology*, **53**, 375–386.
- Stein, R.A. & Magnuson, J.J. (1976) Behavioral response of crayfish to a fish predator. *Ecology*, **57**, 751–761.
- Stich, H. & Lampert, W. (1981) Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature*, **293**, 396–398.
- Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, **73**, 747–754.
- Tessier, A.J. & Welsler, J. (1991) Cladoceran assemblages, seasonal succession and the importance of a hypolimnetic refuge. *Freshwater Biology*, **25**, 85–93.
- Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata*, **47**, 3–14.
- Volkl, W. (1992) Aphids or their parasitoids: who actually benefits from ant-attendance? *Journal of Animal Ecology*, **64**, 273–281.
- Wootton, J.T. & Power, M.E. (1993) Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Sciences of the United States of America*, **90**, 1384–1387.
- Zaret, T.M. (1969) Predation-balanced polymorphism of *Ceriodaphnia cornuta* Sars. *Limnology and Oceanography*, **14**, 301–303.
- Zaret, T.M. (1972a) Predator–prey interaction in a tropical lacustrine ecosystem. *Ecology*, **53**, 248–257.
- Zaret, T.M. (1972b) Predators, invisible prey, and the nature of polymorphism in the cladocera (class crustacea). *Limnology and Oceanography*, **17**, 171–184.
- Zaret, T.M. & Suffern, J.S. (1976) Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography*, **21**, 804–813.

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