How predictable are the host ranges of parasitoids?

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Spectrum of Host Specificity in Parasitoids

Generalists– tachinid-*Compsilura concinnata*-200 species in many families

Family level specialists- sciomyzid fly *Pelidnoptera nigripennis* (F.) (Julidae), the dryinid *Neodryinus typhlocybae* (Ashmead) (Flatidae), tachinid *Aphantorhaphopsis samarensis* (Lymantriidae)

Subfamily/tribe specialists- tachinid *Celatoria compressa* (Galerucinae)

Genus specialists- *Cotesia glomerata* (L.) (Pieris); *Phymastichus coffea* (*Hypothenemus*)

Monospecific species- *Cotesia rubecula* (Marshall) (*Pieris rapae*) *Lathrolestes nigricollis* (? just *Fenusa pumilla*)

Context dependent safety- where to draw the line depends on fauna of region receiving introduction

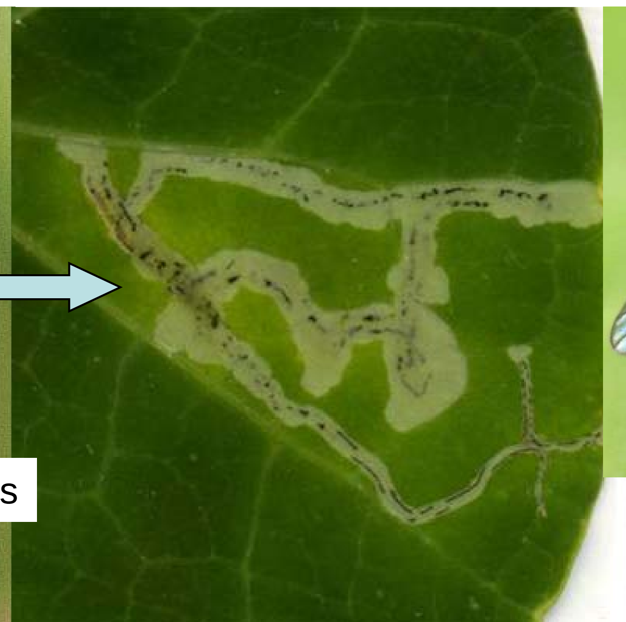
Section 1: Correlates of host range

(1) *phylogeny*

(2) *shared ecology*

(3) *nature of host defenses*

Dacnusinae (Braconidae) parasitoids limit their attack to various (not all) agromyzid leafminers. For example, *Dacnusa sibirica* is an internal parasitoid of many *Liriomyza* spp. Leafminers in this genus are all polyphagous, such that the plant provides no constant signal useful to the parasitoid to discover its host.



Leafmine of *Liriomyza bryoniae*

Dacnusa sibirica

Correlates of host range

(1) *phylogeny*

(2) *shared ecology*

(3) *nature of host defenses*

Some external larval parasitoids may accept as hosts insects in leafmines with similar morphology on similar trees even if the actual leafminers are quite unrelated taxonomically (different orders).

The driver here is a shared ecology of general form and presentation.

Correlates of host range

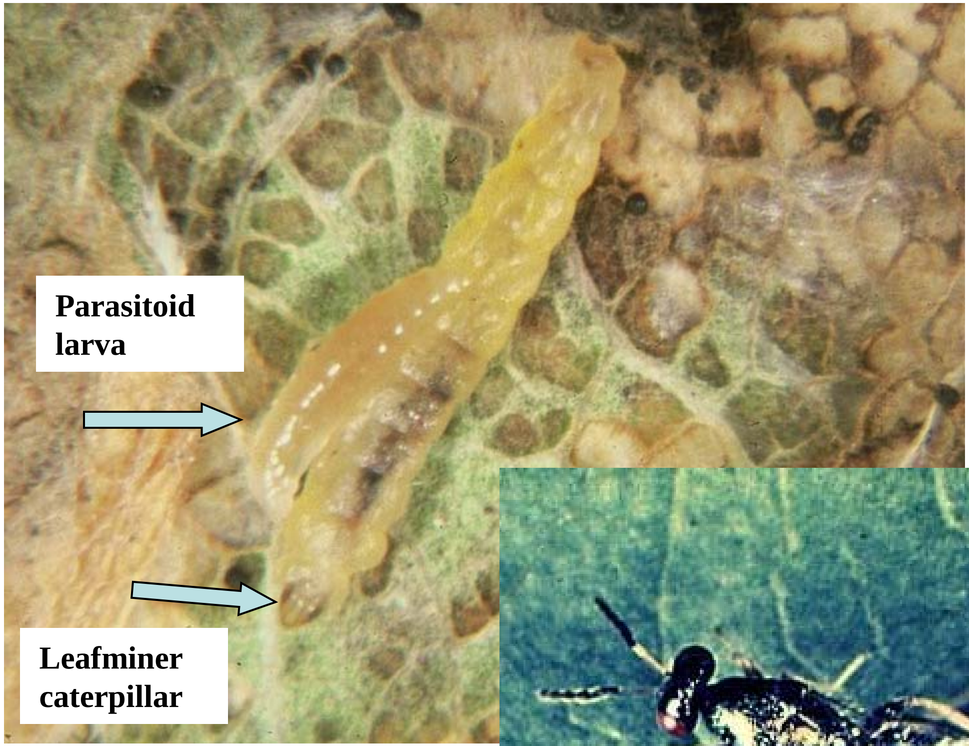
(1) *phylogeny*

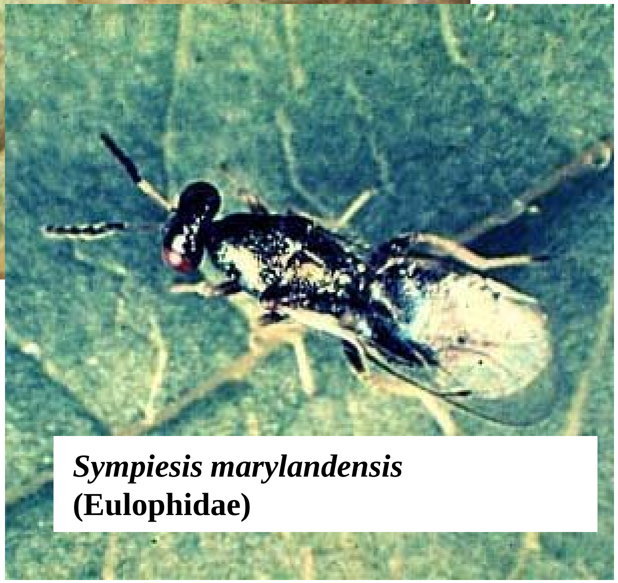
(2) *shared ecology*

(3) nature of host defenses

Idiobionts

- broader host ranges possible
- attack eggs or pupae, which cannot grow
- also, external parasitoids, as these kill their hosts



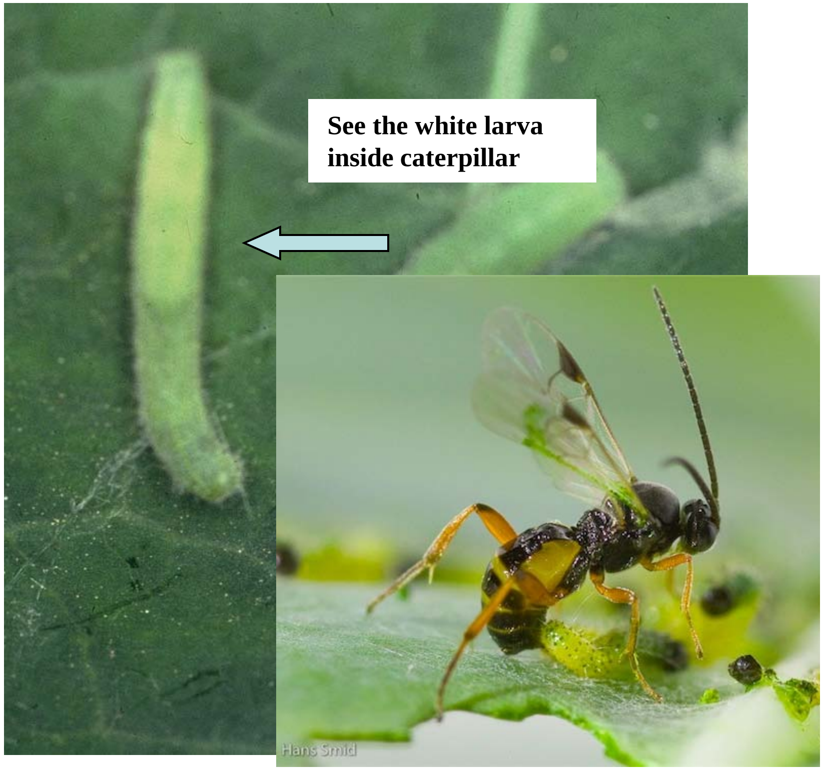


Correlates of host range

(1) *phylogeny*
(2) *shared ecology*
(3) nature of host defenses

Koinobionts

- narrower host ranges because must defeat host defenses
- permit their hosts to continue to grow after oviposition, increasing the resource for progeny
- larval and nymphal parasitoids
- must defeat host immune system



Pieris rapae **larvae. One on left is parasitized by an internal parasitoid,** ***Cotesia rubecula.***

Section 2-
Host range of what exactly?

A. Strongly differentiated, morphologically distinct species

B. Cryptic species (biotypes)

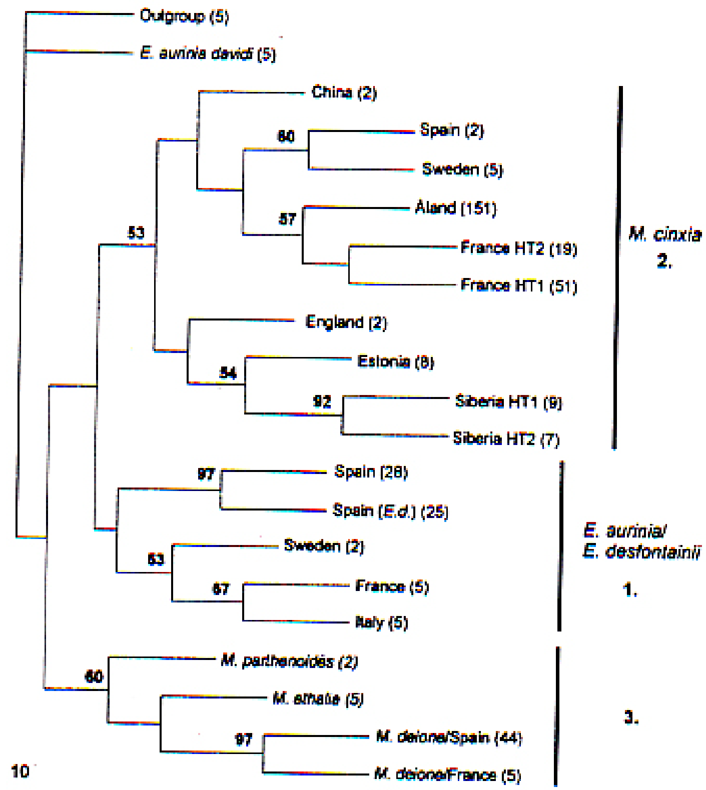
- -Host-adapted entities
- -Geographically specialized entities

Host-adapted entities -example 1

checkerspot parasitoids in Finland

Melitaea cinxia

Euphydryas aurinia



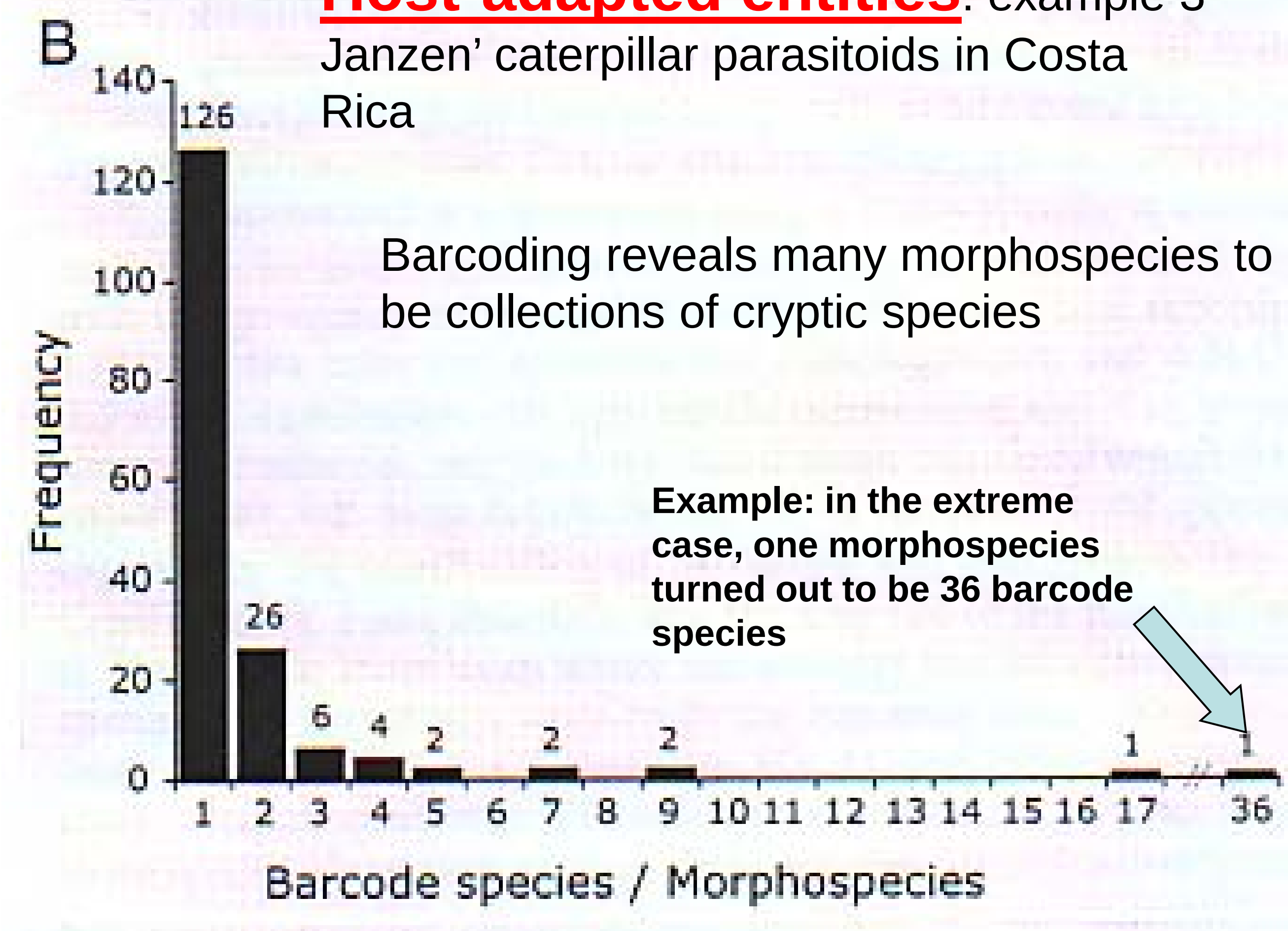
Cotesia melitaearum

One species or two?

Two host-specialized races of *Cotesia melitaearum*

Kankare et al., 2005 Ann. Entomol. Soc. Am 98: 382-394

Host-adapted entities: example 3- Janzen' caterpillar parasitoids in Costa Rica

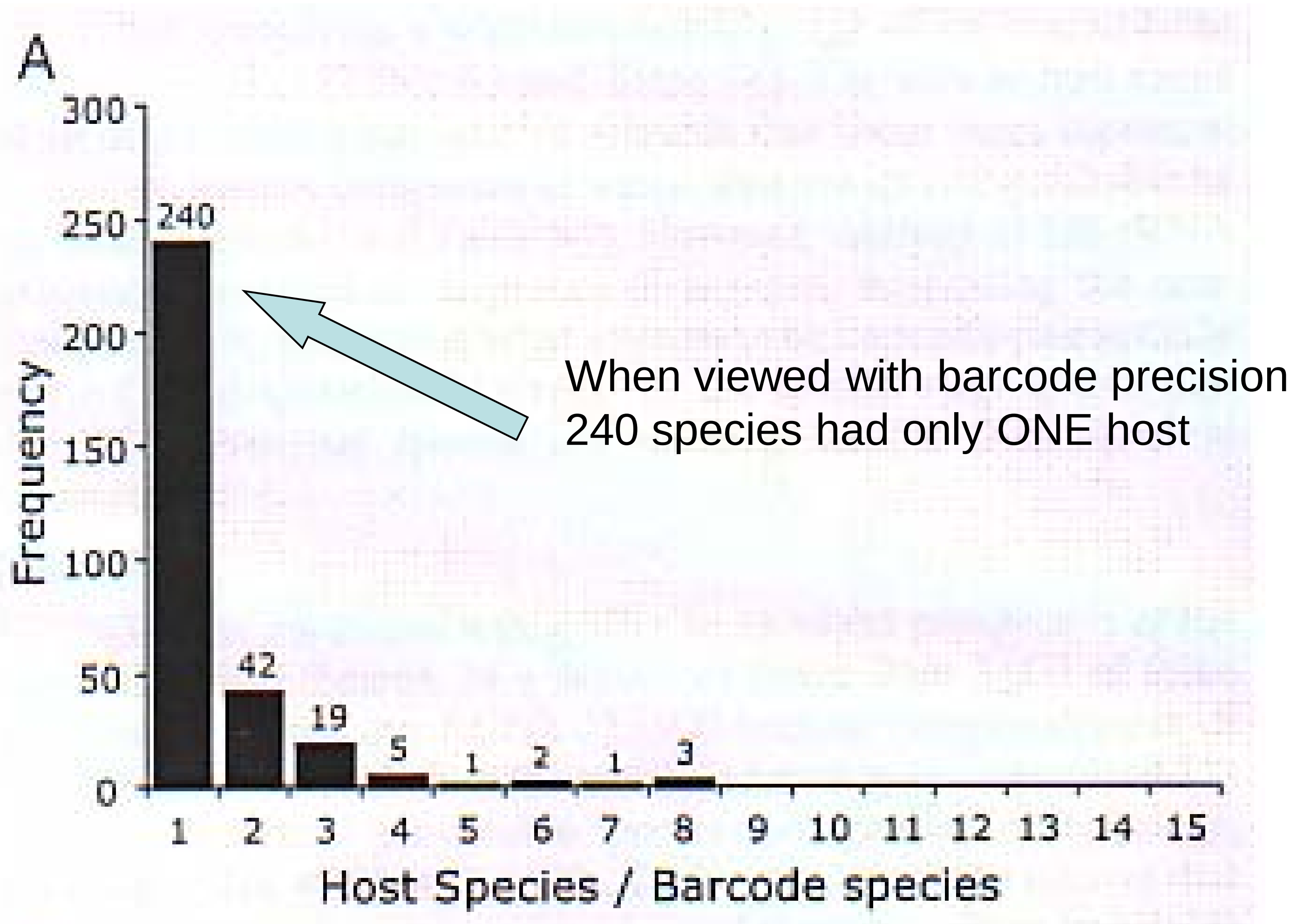


Barcoding reveals many morphospecies to be collections of cryptic species

Example: in the extreme case, one morphospecies turned out to be 36 barcode species

For Hymenoptera parasitoids, in the Janzen study, here we see that many provisional morphospecies broke apart into many species when barcoded. One morphospecies became 36 species!

From White et al., 2008, PNAS 105: 12359-12364

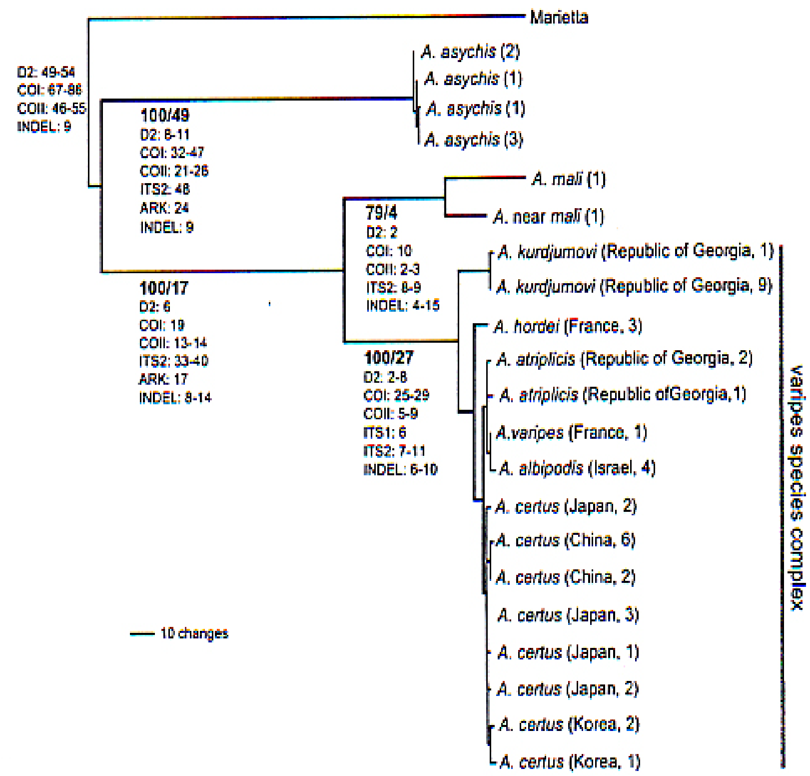


For Hymenoptera parasitoids, in the Janzen study, here we see the number of hosts per "barcode species" suggesting that >90% of the parasitoids studied (of 313 species) usually had only one host, and no more than two.

From White et al., 2008, PNAS 105: 12359-12364

<u>**Geographically differentiated entities**</u> -example 1

Russian wheat aphid parasitoids in the *A. varipes* complex



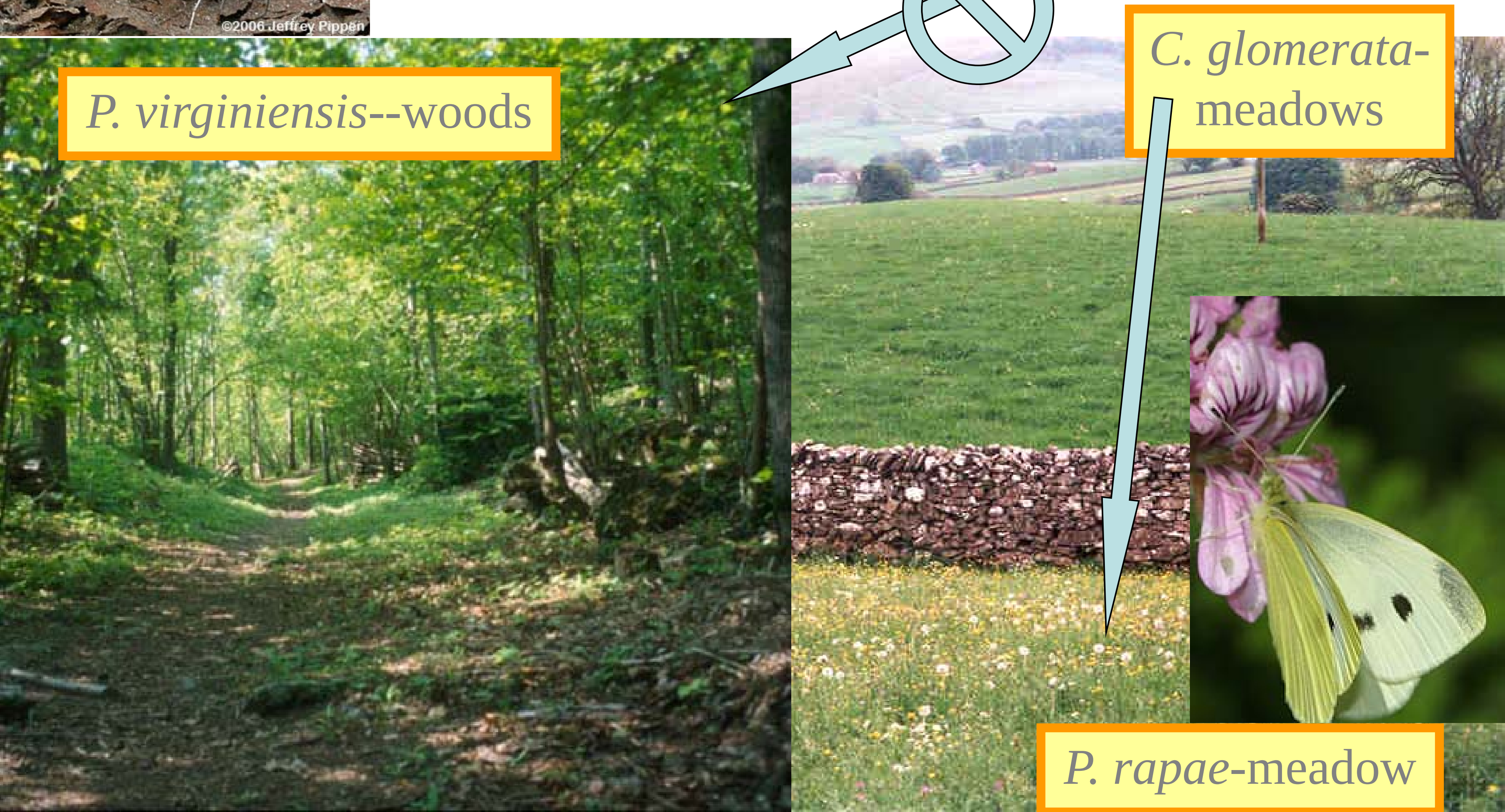
Aphelinus varipes- **from 1 species to 5 geographically differentiated species**

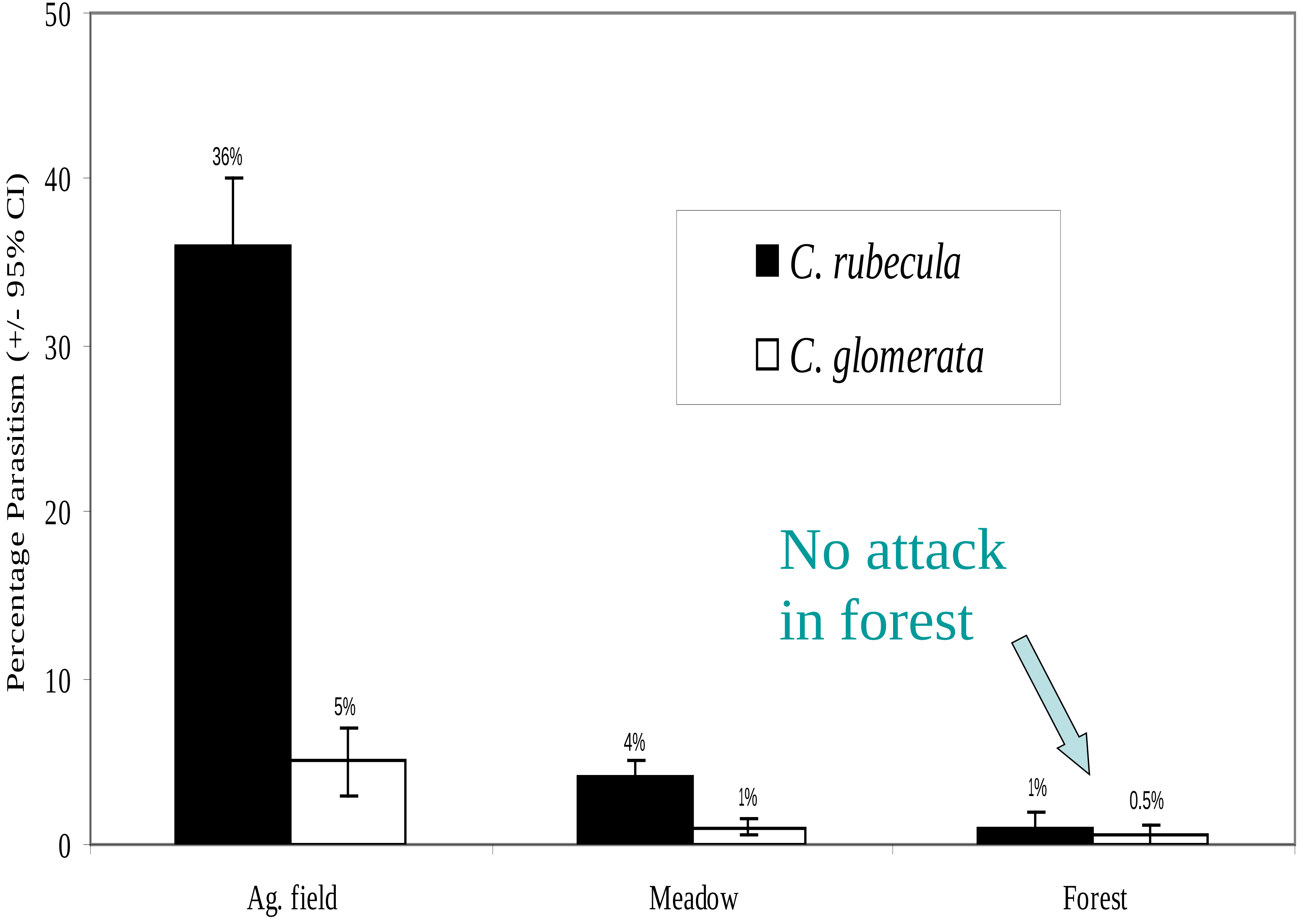
Heraty et al., 2007 Mol. Phylogenetics and Evol. 45: 480-493

Section 3.
Filters that shape host ranges

1. Pest habitat
2. Odors from host/plant complex
3. Attractive chemicals from host
4. Effects of parasitoid learning
5. Host defenses against parasitoids

Filter #1. HABITAT




Percentage Parasitism (+/- 95% CI)
50
40
30
20
10
0
36%
5%
4%
1%
1%
0.5%
C. rubecula
C. glomerata
No attack
in forest
Ag. field
Meadow
Forest

FILTER #2. THE HOST PLANT

The adult parasitoid may find hosts by moving toward odors of its host's characteristic plant

Example: crucifers produce **mustard oils** and their breakdown products, which are highly attractive to *C. glomerata*

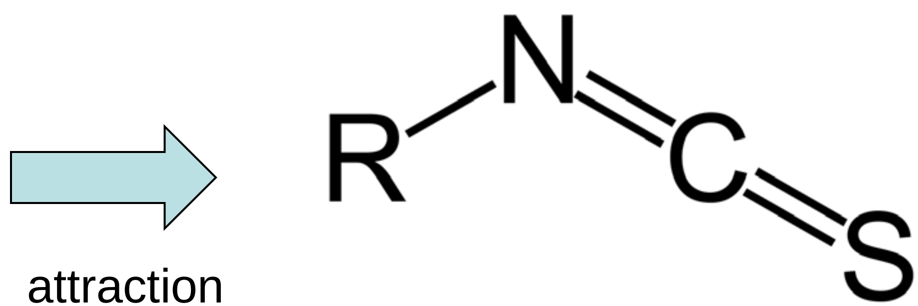


Table 1. Examples of parasitoids that seek their characteristic hosts via their attraction to the odors of the insect's host plant.

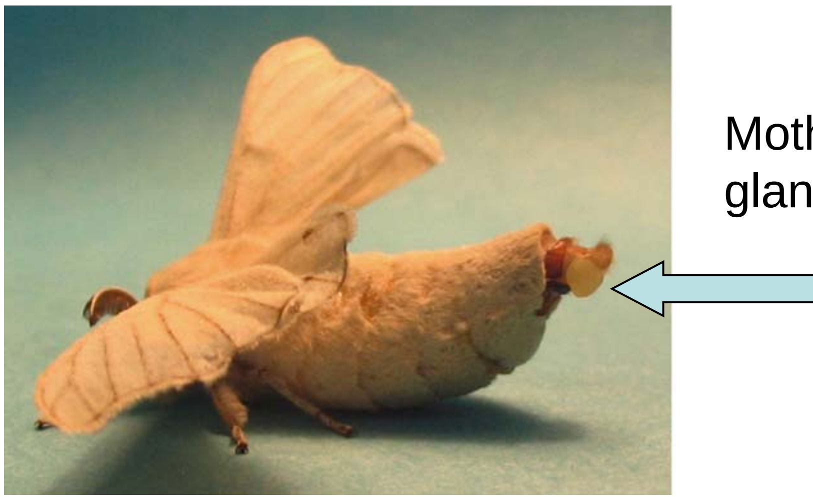
Pest	Host plant	Chemical	Parasitoid	Reference
Brevicoryne brassicae (L.)	Cabbage and other crucifers	Allyl isothiocyanate	*Diaeretiella rapae* (M'Intosh)	Read et al., 1970
Trupanea dubautiae (Bryan)	*Dubautia raillardioides*	Native HI composite shrub NOT attractive to introduced parasitoids	*Diachasmimopha longicaudata* (Ashmead) and *Psyttalia fletcheri* (Silverstri)	Duan and Messing, 1997
Macrosiphum rosae L.	*Rosa* spp.	Rose odor	*Aphidius rosae* Haliday	Kitt and Keller, 1998
Agrilus planipennis Fairmaire	Ash (*Fraxinus* spp.)	Ash volatiles	*Spathius agrili* Yang	Yang et al., 2008
Acrolepiopsis assectella (Zeller)	Leeks and garlic (*Allium* spp.)	Volatile sulfur compounds from leeks	*Diadromus pulchellus* Wesmael	Mason, 2009.

Plant-entrained entities

Since *C. glomerata* is attracted to odors from crucifers, pierids in Chile that have moved over to legumes are probably outside its host range

Since *Spathius agrili* is attracted to ash volatiles, *Agrilus* spp. attacking non-ash are probably outside its host range

FILTER #3. (Adult): Attraction of the parasitoid to compounds emitted by the insect host

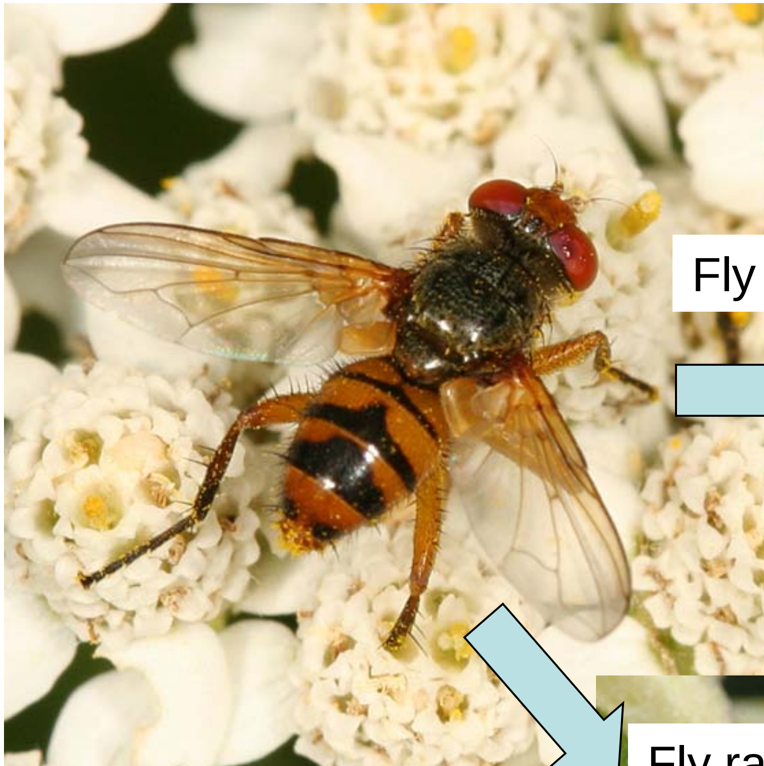


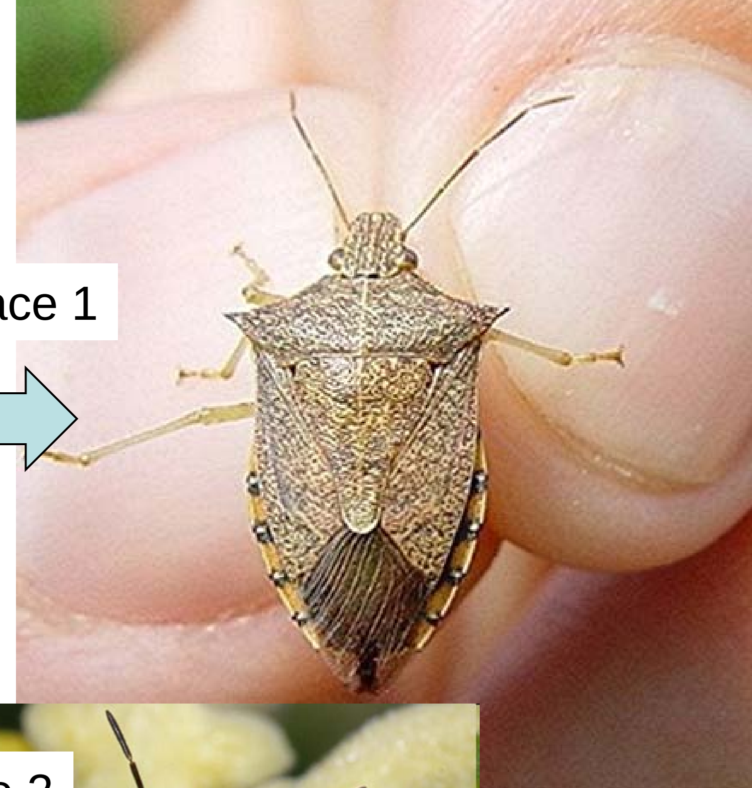
Moth emitting pheromone from gland while calling males

In some systems, parasitoids with narrow host ranges use their host's **sex pheromones** to locate them.

Table 2. Examples of parasitoids that seek their characteristic hosts via their attraction to the pests pheronomones.

Pest	Kind of pheromone	Parasitoid	Reference
Quadraspidiotus perniciosus (Comstock)	sex pheromone	*Encarisa perniciosi* (Tower)	Rice and Jones, 1982
Helicoverpa zea (Boddie)	sex pheromone	*Trichogramma pretiosum* Riley	Lewis et al., 1982; Noldus et al., 1990
Ostrinia nubilalis Hübner	egg mass and scale volatiles, sex pheromone	*Trichogramma ostriniae* Pang and Chen	Yong et al., 2007
Sesamia calamistis Hampson	adult females (sources of sex pheromone)	*Telenomus busseolae* (Gahan) and *Telenomus isis* (Polaszek)	Fiaboe et al., 2003
Podisus spp. or *Euschistus* spp. depending on fly strain	aggregation pheromones	*Euclytia flava* (Townsend)	Aldrich and Zhang, 2002
Paraponera clavata (Fabricius).	alarm pheromone	*Apocephalus paraponerae*	Feener et al., 1996, Morehead et al., 2001





The tachinid *Euclytia flava* finds its bug hosts by tracking their **aggregation pheromones**. This tachinid has cryptic races that track either *Podisus* spp. (predators) (upper right) or *Euschistus* spp. (herbivores) (lower right)

Filter 4. (Adult): Effects of learning by adult parasitoids

Generalist parasitoids are quicker learners than specialists

Hans M. Smid
PhD 1998, Wageningen University

Cotesia glomerata

"My research focuses on the role of associative learning in two closely related species, the generalist *Cotesia glomerata* and the specialist *Cotesia rubecula*. **Both wasp species can learn** to associate plant odors of a particular plant with the host. **However, *C. glomerata* can learn very fast**, it forms long term memory after a single learning experience, whereas *C. rubecula* learns slow; it needs several repeated experiences before it forms long term memory."

Consequence for BC-if we use specialists, learning will have little influence on outcomes

Filter 5. Host defenses.

A species will only be a host if the parasitoid can defeat its defense

Cross section of two parasitoid eggs surrounded by blood cells

Importance to biocontrol safety: Some nontarget species may occasionally be oviposited in, but if parasitoids fail to develop due to host defense, no population level effects on the nontarget species are likely

Black dots are melanized parasitoid eggs killed by encapsulation

Section 4.
List Checking vs Estimating fundamental host ranges

List checking

Est. Fund. Host ranges

Eat species A, B, C?

Prediction of genera or species at risk

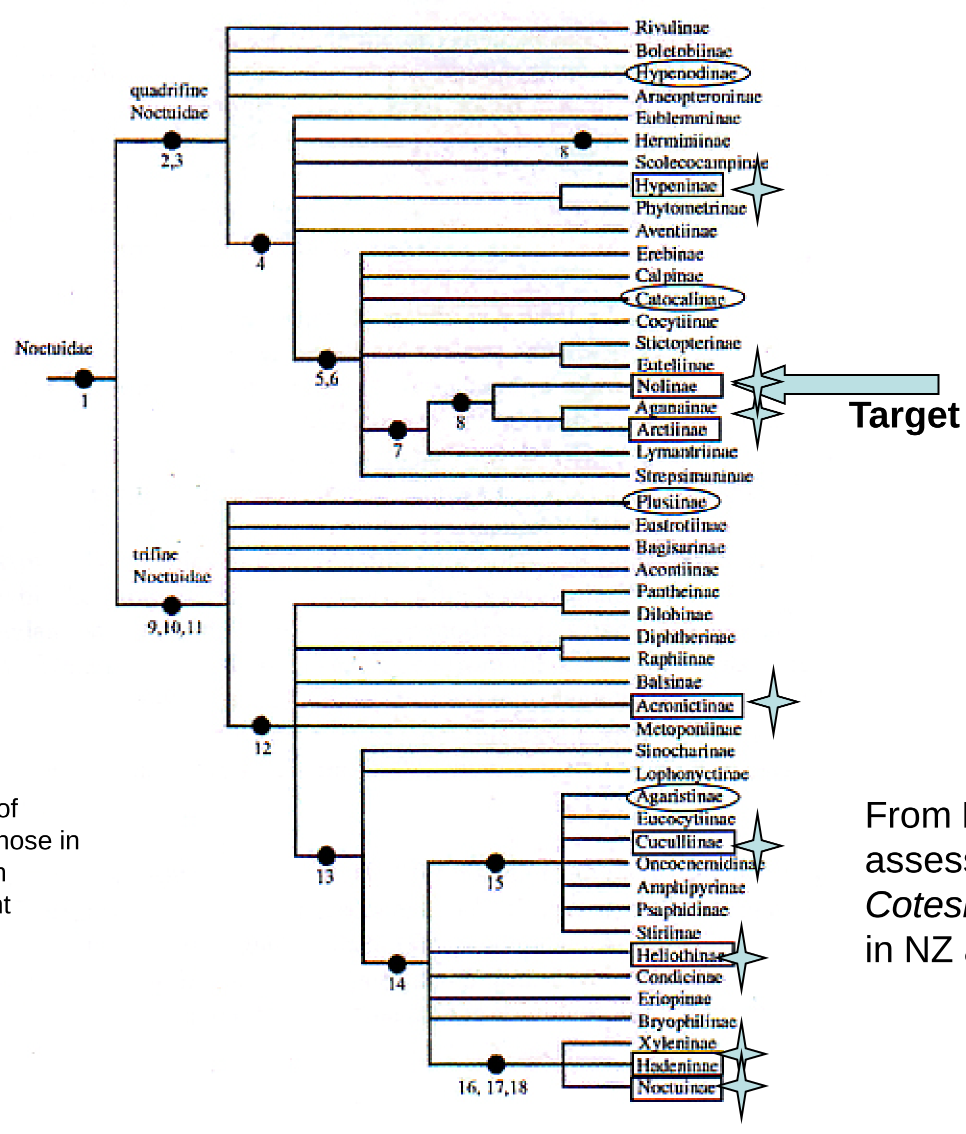
Defining the test list

1. **Safety species** (special economic or ecological concern in area)

2. **Related species** (phylogenetic or ecological relatedness to target pest)

Related Species – species chosen to find boundaries of host range

Use of phylogeny of Noctuids to frame test species selection



Target pest is in Nolinae

Boxed subfamilies contain endemics of special interest in release area (NZ); those in ovals have only exotic or cosmopolitan species. Other subfamilies not present

From Berndt et al. 2010, for assessing host range of *Cotesia urabae*, for release in NZ against *Uraba lugens*

Criteria being used by Mark Hoddle to screen parasitoids of citrus psyllid

- Phylogenetic relatedness to the pest
- Native (CA) psyllids that use native plants in the same family as citrus (Rutaceae)
- Native CA psyllids found on native plants common in undeveloped areas bordering citrus orchards (e.g., *Ceanothus* & its suite of psyllids)
- Common pest psyllids (because it is easy to do so)
- Psyllids that are weed biocontrol agents (because this is being responsible)

Tests most likely to be used with parasitoids

1. Attraction to volatiles

2. Oviposition tests with nontargets

3. Survival and development of immatures

TEST DESIGNS

1. **no choice—** **for adult oviposition and follow thru for immature survival in host**

2. **choice (preference)** **(may be sequential)**

Sequential choice tests with *Pseudacteon curvatus* and native (*S. geminata*) vs imported fire ants (*S. invicta*)

Fly species	**No. attacking flies and attack rate per fly**		
	Time 1-- *S. invicta*	Time 2 -- *S.geminata*	Time 3-- *S. invicta*
P. litoralis	23/23 2.33 attacks/fly	2/23 0.34 attacks/fly	20/21 1.11 attacks/fly
P. wasmanni	18/18 3.21 attacks/fly	2/18 3.1 attacks/fly	8/13 3.0 attacks/fly
P. tricuspis	25/25 1.91 attacks/fly	1/25 0.04 attacks/fly	15/21 1.17 attacks/fly
P. curvatus	20/20 1.53 attacks/fly	13/20 0.75 attacks/fly	--

From Gilbert and Morrison 1997 Environ. Entomol. 26: 1149-1154

Section 4.
Post-release monitoring

- Does attack happen on non-target in the field?
- Multiple years/sites
- Trivial attack
- Experiments to assess importance of non-trivial attack

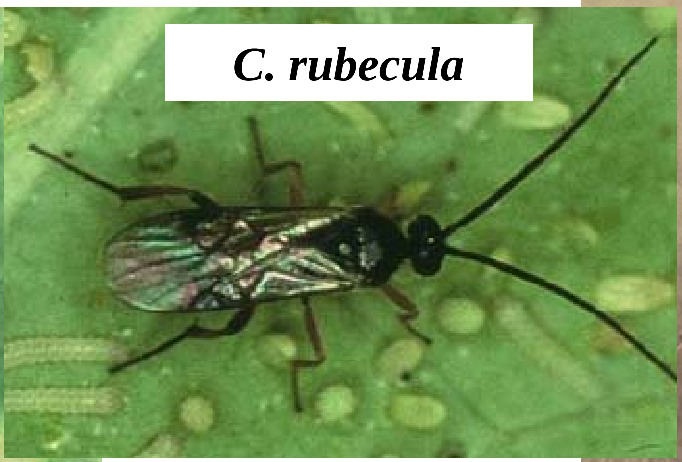
Post release monitoring example #1
Native NZ weevils and *Microctonus aethiopoides or M. hyperodae*

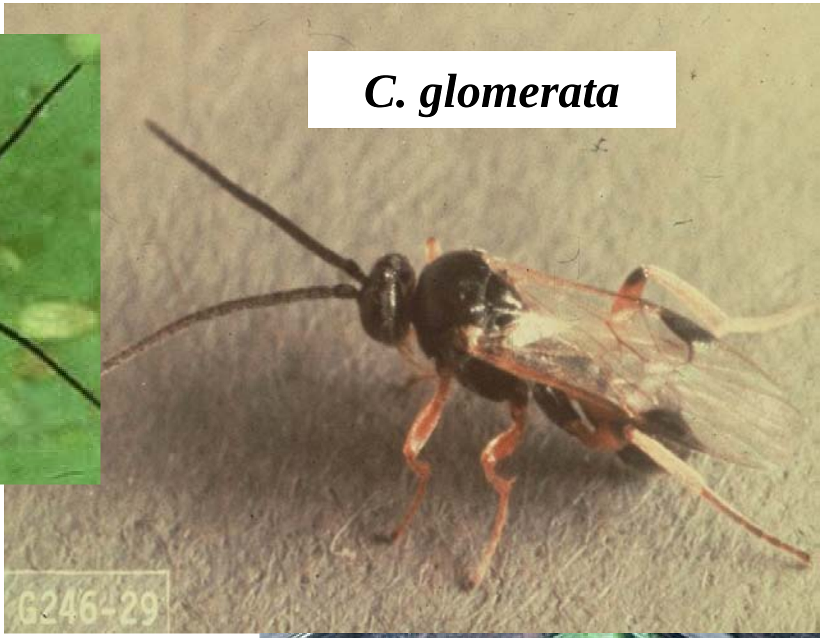
	Parasitoid species	
	M. aethiopoides	*M. hyperodae*
Laboratory tests		
No. nontarget species parasitized (no. tested)	12 (13)	7 (30)*
No. nontarget genera parasitized (no. tested)	9 (11)	3 (21)*
No. tribes parasitized (no. tested)	4 (5)	1 (4)*
No. subfamilies parasitized (no. tested)	2 (2)	1 (2)*
Mean % parasitism of nontarget hosts (target host)	58 (62)	13 (61)
Mean % showing immune response in nontarget hosts (target host)	12 (0)	32 (2)
Field monitoring		
No. nontarget species parasitized (no. examined)	14 (48)	2 (48)
No. genera parasitized (no. examined)	8 (23)	2 (18)
No. tribes parasitized (no. examined)	4 (8)	1 (7)
No. subfamilies parasitized (no. examined)	2 (2)	1 (2)
Mean % parasitism recorded (range)	23 (0–71)	1.8 (0–3)
No. sites where nontarget parasitism was found (total sites sampled)	17 (33)	1(33)

*Includes (Goldson et al. 1992) data.

Post release monitoring example #2
Cotesia spp. and native *Pieris* butterflies in MA

Larvae of *Pieris rapae*, the imported cabbageworm

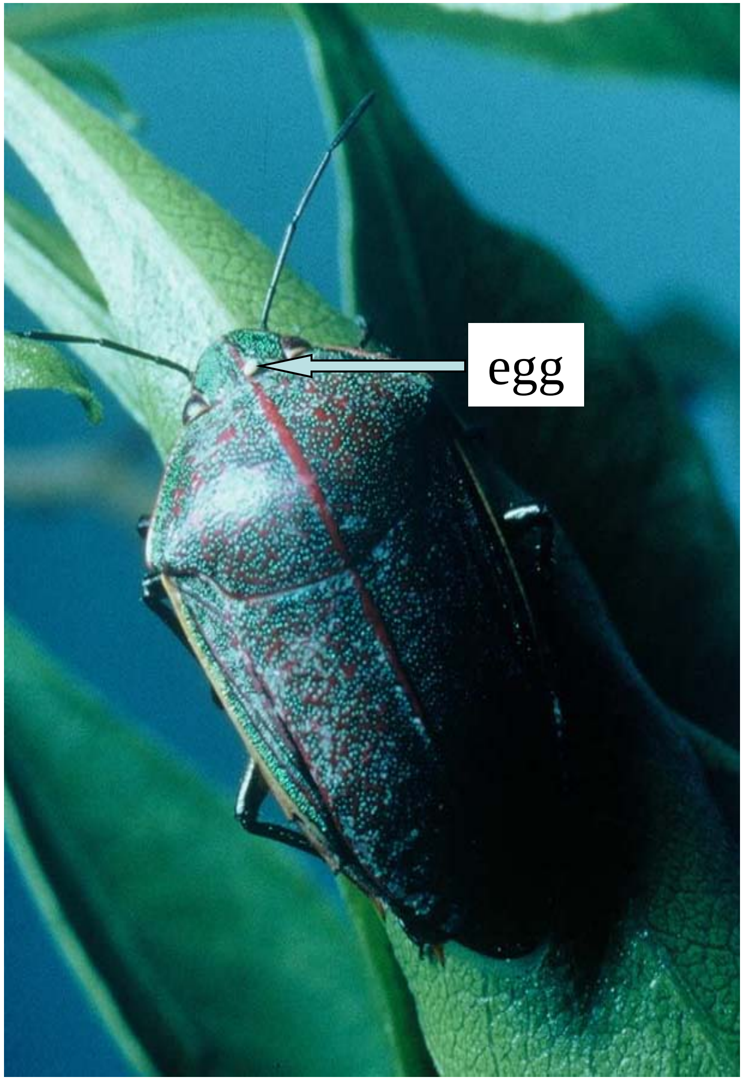




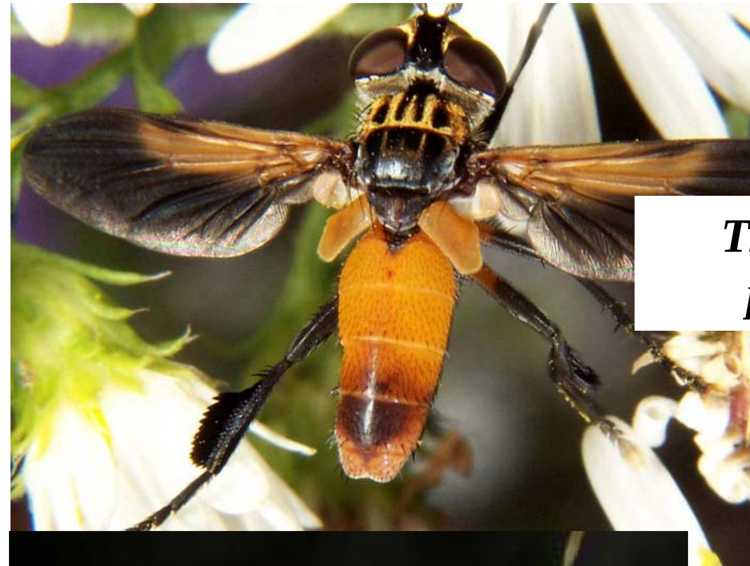
Attack rates of *Cotesia glomerata* and *C. rubecula* in choice tests in lab (L) vs field (F)

	Pieris napi	*Pieris rapae*	***napi*--*rapae* ratio**	Is lab predictive of field outcome?
Cotesia glomerata	L 52 ± 6.9% (201) F 24 ± 2 (2214)	L 24 ± 6.1% (189) F 5 ± 1 (3336)	**2.2 L** **4.8 F**	Yes-*napi* strongly preferred in field
Cotesia rubecula	L 49 ± 6.8% (210) F 3 ± 1 (291)	L 67± 6.5% (198) F 21 ± 2 (245)	**0.7 L** **0.1 F**	No- *napi* scarcely attacked in field

Post release monitoring example #3. ***Trichopoda pennipes*** **released against green stink bug in HI with nontarget attack on koa bug**



Koa bug, the native species attacked



Trichopoda pennipes

***Nezara viridula*, the target pest**

Museum records (eggs on pined bugs) as evidence for parasitism of native HI Hemiptera by *T. pennipes*

Table 1. *Trichopoda* eggs on Hawaiian museum specimens of pentatomoids collected between 1965 and 1995[1].

Taxon	N	Parasitized	%
ALIEN PENTATOMIDAE			
Nezara viridula	302	52	17.2
Plautia stali	160	7	4.4
Thyanta custator accerra	58	3	5.2
Brochymena quadripustulatus	62	1	1.6
Eysarcoris ventralis	3	0	0.0
NATIVE PENTATOMIDAE			
Oechalia pacifica	64	0	0.0
O. virigula	12	0	0.0
O. virescens	9	0	0.0
O. grisea	4	0	0.0
O. patreulis	4	0	0.0
O. hirtipes	3	0	0.0
NATIVE SCUTELLERIDAE			
Coleotichus blackburniae	107	9	8.4

"The impact of *T. pilipes* on *C. blackburniae* appeared to be low overall, with mean parasitism near zero in most habitats. Mean parasitism exceeded 10% only in one host plant, only at moderate elevations"

Field study of parasitism of koa bug in Hawaii 1998-1999

Insect species	Host plant	Elevation of sites (m)	Percent parasitism[a], mean per site	
			Male adults	Female adults
C. blackburniae	*Dodonaea viscosa*	60–360	3.6 (1)	0 (1)
		600–1,100	31.2 ± 13.1 (3)	12.0 ± 7.4 (4)
		1,500–2,050	1.2 ± 0.8 (6)	0 (6)
	Acacia confusa	10–300	7.2 ± 6.0 (4)	5.3 ± 3.9 (4)
	Acacia koa	760–1,200	0 (1)	0 (1)
		1,960	0 (1)	0 (1)
N. viridula	*Crotalaria* spp.	60–100	70.0 ± 13.3 (2)	47.1 ± 14.8 (2)
	Ricinis communis	800–1,000	40.2 ± 30.3 (2)	11.9 ± 9.5 (2)

Johnson et al. (Oecologia 2005: vol 142, pp 529-540)

Some post-release studies have, however, found evidence of large, significant impacts of some biocontrol parasitoids

Impacts of the tachinid *Compsilura concinnata on* native saturnids

A tachinid fly introduced in 1905 to control gypsy moth an browntail moth

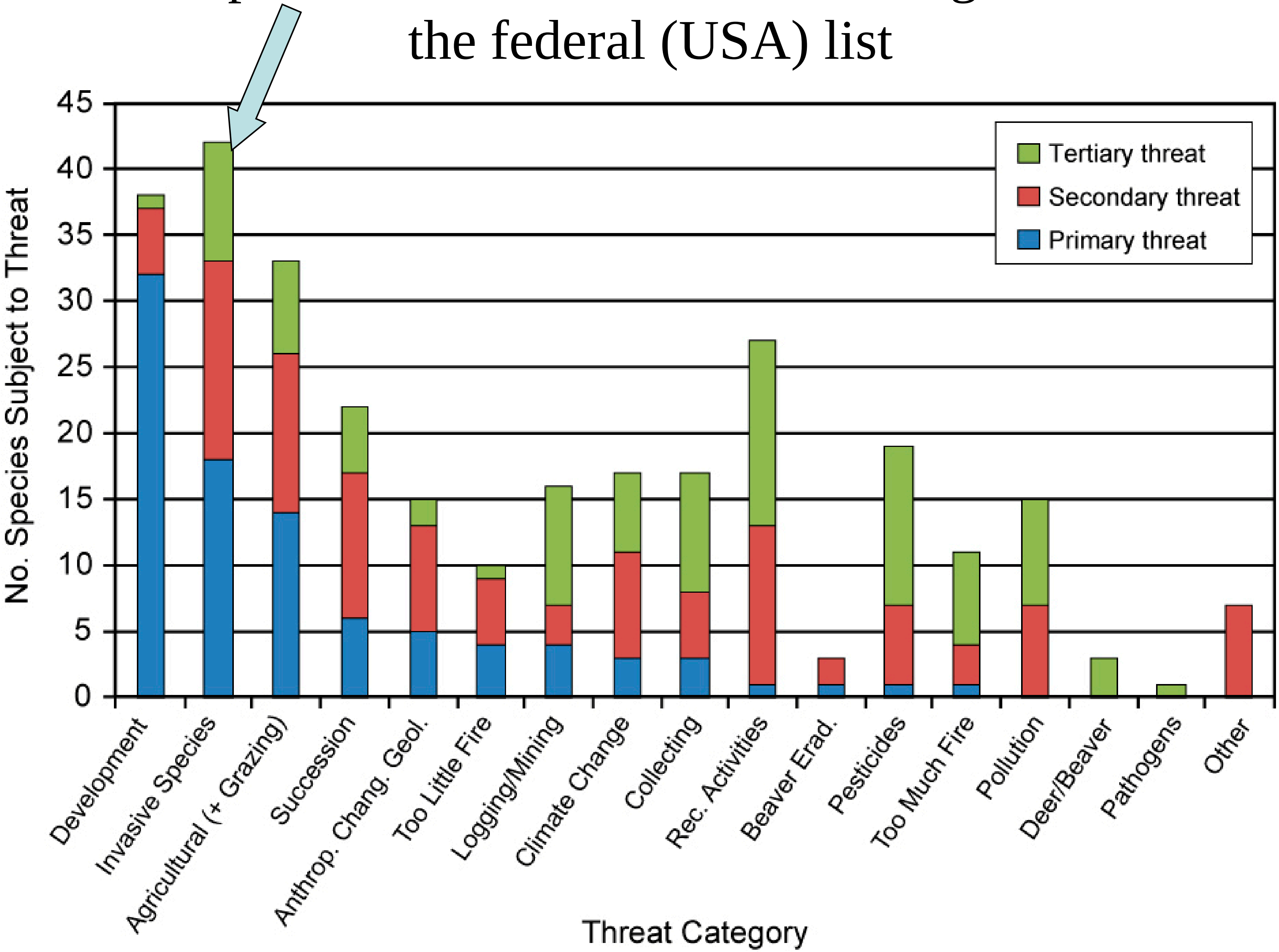


Layout	No/tree	Deployed	Recovered	Compsilura mortality
Inland				
Transect	1	68	39	38.5%
Transect	5	100	55	56.6 %
Clumped	1	70	52	82.7%
Clumped	5	100	74	84.9%
Coastal				
Transect	1	63	38	10.5%
Transect	5	95	42	35.7%
Clumped	1	40	19	47.4%
Clumped	5	100	31	13.8%

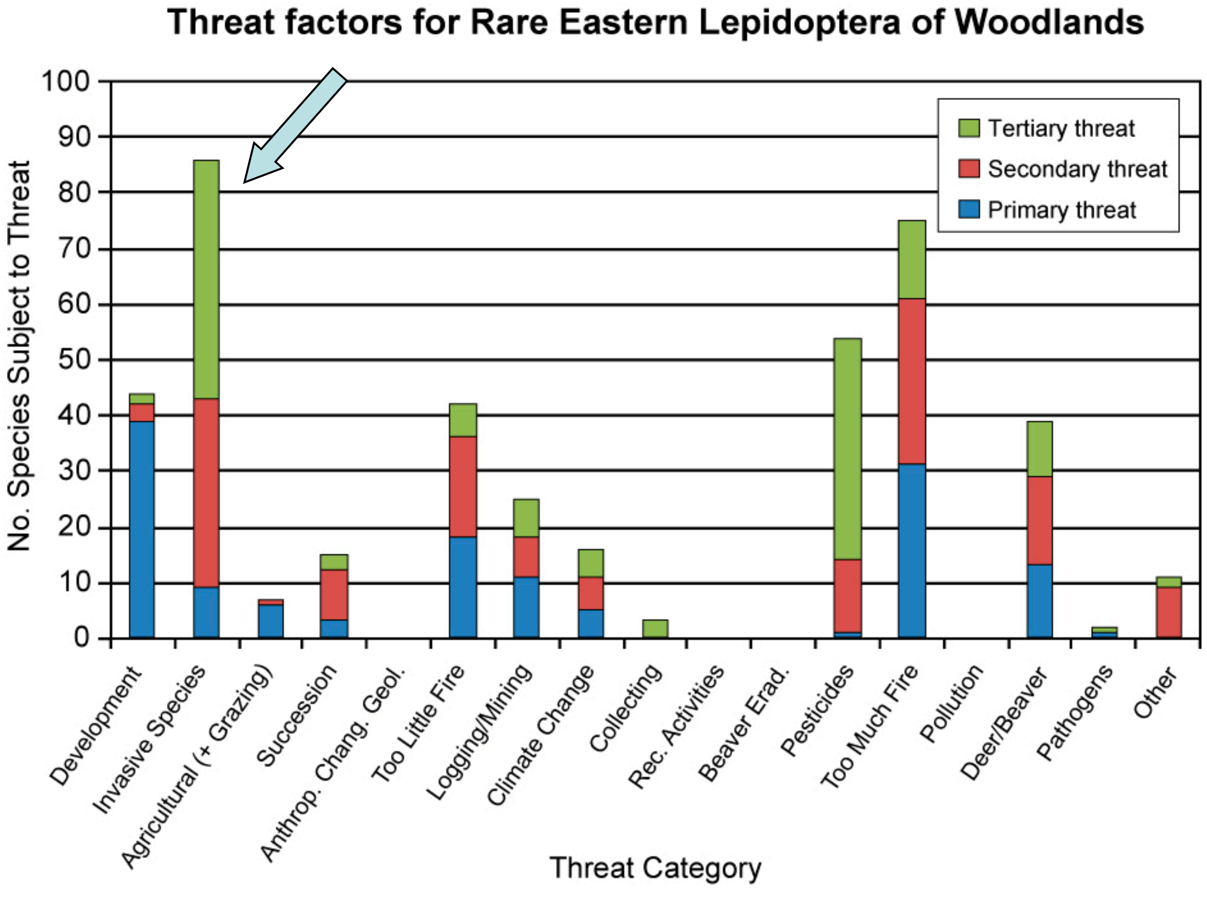
Note: no native flies at any site.

Section V.
Are biocontrol agents an important threat endangering native insects?

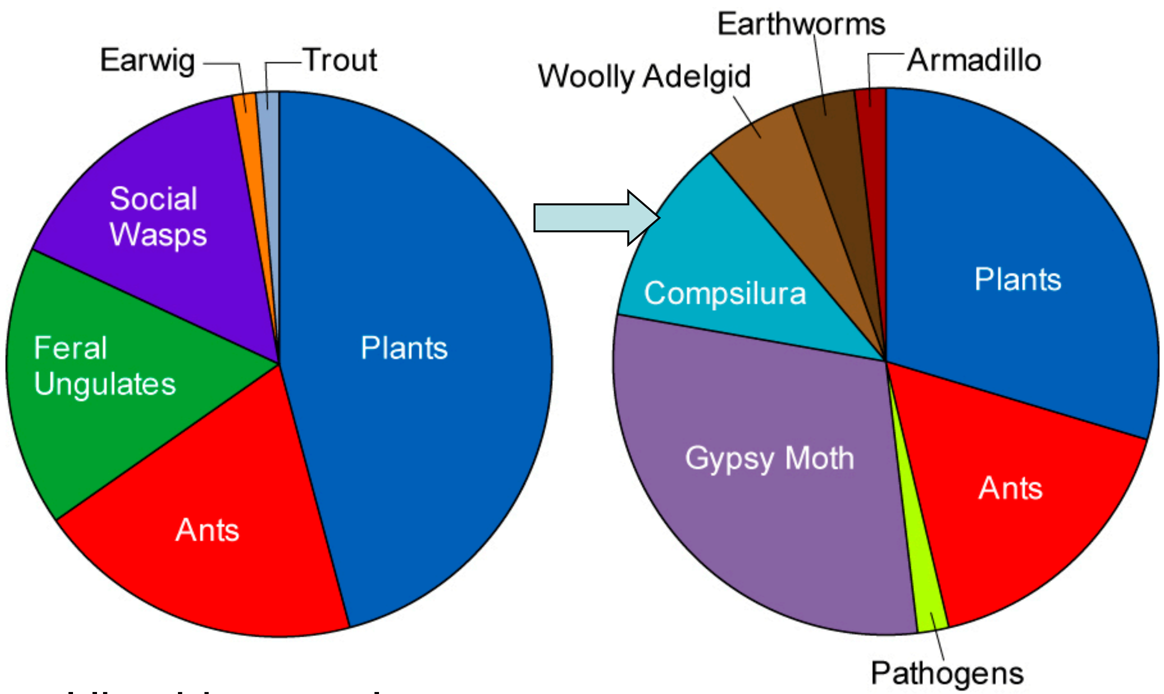
Invasive species are the #2 threat to endangered insects in the federal (USA) list



And invasive species are the #2 threat to endangered Lepidoptera in the eastern USA



But among invasive species endangering insects, biocontrol agents are not an imporant risk factor except in one case



Federal list, biocontrol agents not important cause of endangerment

NE US Lep list, one biocontrol agent, *C. concinnata*, is imporant

Conclusions

- Prediction of parasitoid host ranges is complex but possible
- Issues to consider when doing so
  - (a) beware of literature records
  - (b) obtain parasitoid from target pest
  - (c) confirm monophyletic nature of source population
  - (d) check attraction to host plant or host itself
  - (e) proceed with tests as used for herbivores
- **Rise above list checking and aim for estimation of the fundamental host range**