Can a pathogen provide insurance against host shifts by a biological control organism?

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Summary

The cinnabar moth, Tyria jacobaeae (L.) (Lepidoptera: Arctiidae), is an icon in population ecology and biological control that has recently lost its shine based on evidence that (a) it is less effective than alternatives (such as the ragwort flea beetle Longitarsus jacobaeae (Waterhouse) Coleoptera: Chrysomelidae) for controlling ragwort, Senecio jacobaea L. (Asteraceae), (b) it eats (harms) non-target plant species (including arrowleaf ragwort, Senecio triangularis Hook. (Asteraceae), a native North American wildflower, and potentially harms the animals that depend on these native plant species and (3) it carries a disease (caused by a host-specific microsporidian Nosema tyriae). We used a life table response experiment (LTRE) combining a factorial experiment and a matrix model to estimate the independent and interacting effects of Old World and New World host plant species (first trophic level) and the entomopathogen (third trophic level) on the life cycle and population growth of the cinnabar moth (second trophic level). Host shifts are expected if herbivore fitness is higher on novel compared with conventional host plants, perhaps because the advantage of reduced effectiveness of herbivore natural enemies outweighs the disadvantage of herbivore malnutrition associated with novel host plants. Contrary to this hypothesis, we found the population growth rate of the cinnabar moth is sharply reduced on novel compared with conventional host plants by interacting effects of disease and malnutrition. Paradoxically, a pathogen of the cinnabar moth may enhance weed biological control by providing insurance against host shifts.

Keywords: modelling tritrophic interactions, Tyria jacobaeae, pathogen–host interaction, host specificity, microspora.

Introduction

A persistent concern hangs over the practice of classical biological control: If some biological control organisms adopt new hosts, what more can be done to contain them? A growing body of evidence suggests that phytophagous insects commonly adopt new hosts if given sufficient ecological opportunity, genetic variation in traits related to host use and fitness advantage to insects adopting new host plant species (Thompson, 2005). The cinnabar moth, Tyria jacobaeae (L.) (Lepidoptera: Arctiidae), introduced to control ragwort, Senecio jacobaea L. (Asteraceae), matches at least two of three of these requirements: ecological opportunity and genetic variation. The cinnabar moth was introduced to control ragwort on farms in lowlands of the Pacific Northwest in the United States; the unintended consequence was that it ended up feeding on native wildflowers in the mountains. The current distribution of this insect overlaps with potential non-target plant species (ecological opportunity) (Diehl and McEvoy, 1990), populations of the cinnabar moth vary in heritable traits affecting plant use (genetic variation) (Richards and Myers, 1980) and performance of cinnabar moths on one non-target species closely matches that on the target (fitness) (Diehl and McEvoy, 1990). Here we combine observational, experimental and modelling approaches to investigate how an entomopathogen might be used to contain an errant control organism. We use laboratory and modelling studies to show how an entomopathogen might be operating in this system; we use field observations on prevalence of pathogen infection in the wild to document how tritrophic interactions involving an entomopathogen species, an insect species and two plant species are operating in the field. We outline plans for future research emphasizing

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details of transmission. We conclude with implications that this research holds for the science, technology and policy of biological control.

A model system

Biological control of ragwort has been an economic and ecological success along the west coast of North America from British Columbia to Washington, Oregon and northern California (Coombs et al., 1991; McEvoy et al., 1991). Ragwort has declined to 1–3% of its former abundance in that region after introduction of three insect species during a 10-year period: *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae) (cinnabar moth) starting in 1959, *Botanophila seneciella* (Meade) (Diptera: Anthomyiidae) (ragwort seed fly, formerly *Hyloëmia seneciella*) starting in 1966 and *Longetarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae) (ragwort flea beetle) starting in 1969. There is a potential downside as well as an upside to biological control because biological control organisms share attributes of some our worst invaders—capacity to harm, multiply, spread and evolve. The cinnabar moth is not a particularly promising biological control organism. It is less effective than alternatives (such as the ragwort flea beetle *L. jacobaeae*) for controlling ragwort (McEvoy et al., 1993; McEvoy and Coombs, 1999). It eats (harms) non-target plant species (including *S. triangularis*, a native North American wildflower) (Diehl and McEvoy, 1990) and potentially harms the animals that depend on these native plant species. It carries a disease (caused by a host-specific microsporidian, *Nosema tyriae*) (Bucher and Harris, 1961; Hawkes, 1973; Canning et al., 1999). We ask: can we make lemonade out of this lemon?

Circumstances favoring host changes by the cinnabar moth

Quality of life for the cinnabar moth in the New World has declined on its Old World host plant (ragwort). First, the plant resource has collapsed. Under pressure from the ragwort flea beetle, ragwort has declined to 1–3% of its former abundance, leaving little resource for the cinnabar moth. Second, on the plant resource that remains, competitors of the cinnabar moth are overpowering it. The cinnabar moth is an inferior competitor relative to the ragwort flea beetle (McEvoy et al., 1993; McEvoy and Coombs, 1999), but a superior competitor relative to the ragwort seed head fly (Crawley and Pattrasudhi, 1988). Mark–release–recapture studies show that the cinnabar moth is inferior as a colonizer on ragwort relative to both the ragwort flea beetle and ragwort seed head fly (Harrison and Thomas, 1991; Harrison et al., 1995). Thus, there appears to be no possibility of coexistence of cinnabar moth with its competitors on ragwort explained by a colonization/competition trade-off (when an inferior competitor is a superior colonizer). Third, natural enemies of the cinnabar moth abound. Predators (Myers and Campbell, 1976), parasitoids (Cornell and Hawkins, 1993) and pathogens (Hawkes, 1973) have been reported to attack cinnabar moth in North America. One natural enemy, the pathogen *Nosema tyriae*, stands out as more prevalent than the rest, with a median prevalence of 70% measured across 15 populations in the states of California, Oregon and Washington in the United States (Hawkes, 1973). Diet breadth might be the cinnabar moth’s ace in the hole. The fundamental host range (‘physiological host range’) measured in the laboratory includes 132 North American plant species and infraspecific taxa, including 20 species in Oregon (Chambers and Sundberg, 2001). Its realized host range (‘ecological host range’) expressed in the field appears to be much narrower. One candidate to become a new host plant, arrowleaf ragwort *S. triangularis* Hook., stands out above the rest as accessible, acceptable, suitable and vulnerable.

If the quality of life for the cinnabar moth has sharply declined on the Old World host plant species in North America, then would life be better there on a New World host plant species (taking all abiotic and biotic factors into account)?

Tritrophic interactions

We studied interspecific interactions within a tritrophic system consisting of a host-specific pathogen, the microsporidian, *N. tyriae*; the cinnabar moth, *T. jacobaeae*; and two host plants species, the Old World host *S. jacobaea* and the New World host *S. triangularis*.

*Microspora* is a phylum of protozoa found as highly specialized, obligatory, intracellular parasites in nearly all major animal groups, being especially common in insects. They are diverse, with approximately 150 genera containing 1200 species. The disease they cause is called microsporidiosis. They possess unicellular spores, containing a uninucleate or binucleate sporoplasm and an extrusion apparatus always with a polar filament and polar cap. Transmission from one host insect to another occurs both horizontally (oral ingestion; within the same generation) and vertically (mother to progeny; between generations).

Materials and methods

Life table response experiment

We designed and carried out an LTRE (Caswell, 2001) to estimate the independent and interacting effects of two diets (foliage from Old World and New World hosts) and five pathogen levels (doses of 0, 10³, 10⁴, 10⁵ and 10⁶ spores per individual) on cinnabar moth’s life cycle and population growth rate. An
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LTRE combines a factorial experiment and population model as a way of linking environmental conditions, vital rates (rates of growth, development, survival, reproduction and movement) and population dynamics. An LTRE is a powerful way of translating data from individuals to implications for populations, linking a population’s structure with its dynamics and analysing the demographic and population-dynamic consequences of environmental factors.

Methods for a dose–response experiment

We collected cinnabar moth larvae for these experiments from three field sites in western Oregon, USA: Santiam Pass (44°24′08″N 121°51′01″W) in the Cascade Mountains, Basket Slough (44°57′08″N 123°16′09″W) in the Willamette Valley and Neskowin (45°6′23″N, 123°58′46″W) on the Pacific Coast, anticipating that there might be genetic variation in cinnabar moths from different geographic locations that could affect insect–plant interactions. We collected infected larvae from a single population (Neskowin, OR). Infected and uninfected larvae were reared together to facilitate horizontal transmission of the pathogen. Microsporidium spores were isolated from infected larvae and suspended in distilled water at different concentrations (0, 10^3, 10^4 and 10^5 spores/µl). Spore suspensions were stored at 5 ± 2°C for at most 2 months. We used the same mixtures for every test unit (individual larva) regardless of the diet. Nosema tyriae was introduced along with the cinnabar moth, and only a single Nosema sp. (with unusually small spores) is known to occur in this insect. The microsporidium infecting the cinnabar moth collected from Neskowin matches the species description for N. tyriae (Canning et al., 1999). We did not observe any insects infected with Nosema sp. We reared insects under optimal conditions (long day, 16:8 h L/D; temperature, °C, 25:15 L/D; humidity, 90%), reared individually (1 oz cup) and fed them ad lib. There were two diets (foliage of Old World and New World hosts) × five pathogen doses per individual (spore concentrations, 0, 10^3, 10^4 and 10^5 spores) = 10 treatment combinations. We collected New World host plant (S. triangularis) leaves from Mary’s Peak (44°30′16″N, 123°33′00″W). We grew the Old World host plant (S. jacobaea) in our greenhouse in individual pots—natural day lengths, temperature (°C, 25:15 L/D), humidity (90%). Leaves from both plants were fresh. We reared uninfected larvae individually through the first and second instars on both New and Old World host plants and then fed newly molted third instars 2-mm² leaf disks topically treated with 1 µl of each spore dose, corresponding to a pulse of horizontal transmission. We followed insect development daily for nearly two generations, allowing for vertical transmission. We measured vital rates of growth, development, survival and reproduction in response to diet and pathogen treatments.

Construction and analysis of a matrix population model

We constructed and analysed a linear deterministic matrix model \( N(t + 1) = A N(t) \), where \( N(t) \) and \( N(t + 1) \) represent vectors of the abundances in each stage from one time step \( t \) to the next \( t + 1 \) and \( A \) the projection matrix. The life cycle graph (Figure 1) illustrates the eight life cycle stages representing egg, five larval stages, pupa and adult. The life cycle graph also illustrates the 16 life cycle transitions in the model, with seven representing growth \( g \), eight representing stasis \( s \) and one representing fertility \( f \). The time step in the model is 1 day. The life cycle graph can be represented as an \( 8 \times 8 \) matrix \( A \), which, in turn, can be used to project the dynamics.

\[
A = \begin{bmatrix}
  f & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
  g_{s_{1,1}} & s_{2,2} & 0 & 0 & 0 & 0 & 0 & 0 \\
  0 & g_{s_{1,2}} & s_{3,3} & 0 & 0 & 0 & 0 & 0 \\
  0 & 0 & g_{s_{1,3}} & s_{4,4} & 0 & 0 & 0 & 0 \\
  0 & 0 & 0 & g_{s_{2,4}} & s_{5,5} & 0 & 0 & 0 \\
  0 & 0 & 0 & 0 & g_{s_{3,5}} & s_{6,6} & 0 & 0 \\
  0 & 0 & 0 & 0 & 0 & g_{s_{4,6}} & s_{7,7} & 0 \\
  0 & 0 & 0 & 0 & 0 & 0 & g_{s_{5,7}} & s_{8,8}
\end{bmatrix}
\]

The factorial experiment yielded parameter estimates for 20 matrices, one matrix for each of ten

Figure 1. Life-cycle graph showing the eight stages and 16 transitions in the matrix model used to project cinnabar moth population growth. The eight life-cycle stages are egg (E), five larval stages (L1, L2, L3, L4 and L5), pupa (P) and adult (A). The 16 life-cycle transitions in the model include seven representing growth \( g \), eight representing stasis \( s \) and one representing fertility \( f \). The time step in the model is 1 day.
treatment combinations (two diets × five pathogen doses) × two transmission assumptions (case 1, horizontal transmission only; case 2, horizontal and vertical transmission combined). The finite rate of increase $\lambda$, the dominant eigenvalue associated with each matrix, was used as the response variable (population growth rate) in our experiment.

**Results**

**Case 1: Horizontal transmission only**

Population growth rates of the cinnabar moth declined with increasing *Nosema* spore dose; the negative slope of this relationship indicates that the pathogen has adverse effects (Figure 2). The New World host (*S.***

![Figure 2](image-url)

**Figure 2.** The relationship between population growth (finite rate of increase $\lambda$) of the cinnabar moth population and the treatment factors diet (foliage of New and Old Host plant species) and pathogen infection (spore dose) for the case of horizontal transmission only.

![Figure 3](image-url)

**Figure 3.** The relationship between population growth (finite rate of increase $\lambda$) of the cinnabar moth population and the treatment factors diet (foliage of New and Old Host plant species) and pathogen infection (spore dose) for the case combining horizontal and vertical transmission.
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triangularis) was inferior to the Old World host (S. jacobaea) as food; the lower intercept indicates that population growth was lower on New World as compared with Old World host species. The lines for each host are parallel, suggesting that diet and pathogen do not interact in their effects. However, qualitative description of the relationship among population growth, spore dose and host plant species changes when we increase realism by adding vertical transmission.

**Case 2: Horizontal and vertical transmission combined**

When we combined horizontal and vertical transmission, diet and pathogen interacted in their effects (Figure 3). At low spore doses (left side of the graph), there was no detectable effect of pathogen infection in caterpillars on the Old World species and devastating effect of pathogen infection on the New World host species. The host plant species effect was nil in uninfected insects and huge in infected insects. At high spore doses (right side of the graph), the effect of pathogen infection was so overpowering that no effect of diet (host plant species) was expressed.

To summarize the results thus far, mild pathogen infections were devastating on New World host plants and inconsequential on Old World host plants. By contrast, severe pathogen infections were devastating on both New and Old World host plant species.

**Field Observations**

Field prevalence of the pathogen varied with elevation and host plant species (Figure 4). Prevalence declined with increasing elevation (associated with decreasing temperature) over a range in elevation from 0 to 1645 m. At similar elevations, there was a higher prevalence of disease in insects on the Old World host plant species compared with the New World host plant species.

**Discussion**

The strength of the pathogen–insect interaction depends on the plant species—it is weaker on the Old World host (S. jacobaea) than on the New World host (S. triangularis) for mild infections in the laboratory environment. In other words, mild infections are relatively benign in cinnabar moth populations on Old World hosts while comparatively virulent in cinnabar moth populations on New World hosts, under identical optimal laboratory conditions. This asymmetry tilts the odds against the non-target host being more acceptable or more suitable than the target, especially if cinnabar moth is given a choice between Old World and New World host plant species.

A remaining challenge is to reconcile our laboratory and field results. If a pathogen is relatively influential in the laboratory and relatively rare in the field on New World compared with Old World host plants, it would be wrong to conclude that the pathogen is not influential in insects on novel host plants in the field. Pathogens tend to die out as their hosts become rare: but are cinnabar moths rare because of past epizootics, cool temperatures, unsuitable hosts or some other causal factor(s)? Mathematical theory of pathogen–host interactions (Anderson and May, 1981) suggests that (1) there is a minimum, threshold host population size needed for persistence of a pathogen and (2) intermediate levels of virulence are optimal for increase of pathogen prevalence. It follows that higher extinction rates of the pathogen might be expected if, consistent with our observations, the pathogen is more virulent.
and cinnabar moths is rarer (due to some combination of disease and malnutrition) on New World compared with Old World host plants at a given elevation (and corresponding ambient temperature).

Cause and effect cannot be established by passive observation. To investigate a feedback relationship, we need to interrupt the feedback. It would be useful to create an outbreak of cinnabar moths at high elevations and see if microsporidian epizootics develop. It would be useful to know why cinnabar moth populations are smaller at high elevations (>800 m), whether due to past epizootics, cool temperatures or unsuitable hosts. The ability of pathogens to kill ectothermic herbivores has been shown to depend on host body temperature, which fluctuates with environmental conditions (Thomas and Blanford, 2003). The thermal sensitivities of plant, insect and pathogen vital rates must all be taken into account when weighing the outcome of tritrophic interactions. But for the moment at least, it seems that entomopathogens can help prevent non-target effects in the event that an insect biological control agent strays from its target host.

Finding ways to rein in errant classical biological control organisms is likely to be difficult and costly. It is better to predict and prevent adverse effects than to try to mitigate them after the fact. Some scientists worry that new organisms released into the environment are a potent form of pollution: not only with the power to have adverse effects on the environment (like chemicals), but with powers of evolution, replication and autonomous dispersal (unlike chemicals) that make adverse effects harder to predict and manage. The same scientists worry that the epidemic of plant and pest invasions is still not under control. Biological control should help in the war on weeds. Classical biological control has had the advantage over other control methods: it is a technology that operates on a scale that matches the scale of the problem. The obvious bears repeating: do not make things worse by moving the cinnabar moth and other risky control organisms to new geographic areas containing potential non-target species; that would be counterproductive.

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References


