

# Modelling the impacts of two exotic invasive species on a native butterfly: top-down vs. bottom-up effects

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## Summary

1. Exotic invasive species can influence population dynamics of native species through top-down or bottom-up forces. The present study examined separate and interactive effects of multiple exotic species invasions on the native mustard white butterfly, *Pieris napi oleracea* Harris (Lepidoptera: Pieridae), using a stochastic simulation model.

2. *P. n. oleracea* populations in North America have decreased regionally since the 1860s. Competition with an exotic congener (*P. rapae* L.), loss of native host plants and parasitism by the introduced braconid wasp (*Cotesia glomerata* L.), have been suggested to be independently responsible for its decline. The present study examined these hypotheses, as well as an alternative, invasion by an exotic crucifer, garlic mustard (*Alliaria petiolata* [Bieb.] Cavara & Grande).

3. A stochastic simulation model of *P. n. oleracea* population dynamics revealed that decreasing the number of host plants available for oviposition and larval development (i.e. habitat loss), sharply reduced the probability of populations persistence and decreased population size for those that persisted.

4. Simulated invasion by garlic mustard also substantially decreased both probability of persistence (= 0 at approximately 50% cover) and mean population size. Persistence probability never reached zero under any *C. glomerata* scenarios, even when larval mortality in the second generation due to parasitism was 100%. The impact of garlic mustard was intensified by the addition of *C. glomerata* parasitism.

5. Results suggest that bottom-up forces, loss of host plants through forest understorey loss and/or garlic mustard invasion are the most important forces driving *P. n. oleracea* population decline. Parasitism by *C. glomerata* may interact to reduce *P. n. oleracea* populations more rapidly, but appears insufficient alone to cause local extinction.

*Key-words:* extinction, habitat loss, Lepidoptera, population regulation, range retraction, species interactions, trophic cascade.

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## Introduction

Ecologists debate to what extent top-down and bottom-up forces regulate population dynamics (reviewed by Hunter & Price 1992; Power 1992; Hunter, Varley & Gradwell 1997). This debate was initiated by the top-down ‘world is green’ hypothesis proposed by Hairston *et al.* (1960), which maintained that natural enemies control herbivore populations and keep them below densities that would result otherwise in widespread

defoliation. In contrast, the bottom-up view of community regulation, synthesized originally by Murdoch (1966), posits that plant quality and/or quantity limit populations of herbivores and therefore predators. Examples of both patterns have been observed in natural ecosystems (top-down cascades reviewed by Pace *et al.* 1999; Schmitz, Hamback & Beckerman 2000; bottom-up regulatory forces reviewed by Harrison & Cappuccino 1995; Dawes-Gromadzki 2002). Recently, however, research has shifted from quantifying single-direction regulation to exploring the conditions that favour one or the other direction (e.g. Hunter *et al.* 1997; Dawes-Gromadzki 2002; Stadler 2004; Jiang & Morin 2005).

Exotic invasive species can generate bottom-up forces through plant invasion, top-down forces through natural enemy invasion, or forces in either direction from invasion by mid-trophic-level species (Simon & Townsend 2003). Most ecosystems have experienced multiple exotic species invasions at a variety of trophic levels (Mooney & Cleland 2001); consequently, native species might be affected by top-down, bottom-up, or both forces. Our goal was to investigate separate and interactive effects of multiple exotic species invasions on the mustard white butterfly (*Pieris napi oleracea* Harris). *P. n. oleracea* is a member of the *P. napi* L. Holarctic species complex (Opler & Krizek 1984) whose native range in the north-eastern United States has been retracting since the 1860s (Scudder 1889; Longstaff 1912; Klots 1951; Opler & Krizek 1984; unpublished data from Natural Heritage and Endangered Species Program, Massachusetts Division of Fisheries and Wildlife). Several hypotheses have been advanced to explain this range reduction. Scudder (1889), whose correspondents documented disappearances of *P. n. oleracea* during the 1860s and 1870s, thought the decline was due to competition for food with *P. rapae* L., which was introduced from Europe to North America around 1860. However, Chew (1981) found no evidence of interspecific reproductive interference between adults or direct competition between larvae in sympatric populations. Chew (1981) proposed that bottom-up factors, including loss of *Cardamine diphylla* (Michx.) and other native hosts due to woodland destruction, and spread of the exotic weed *Barbarea vulgaris* (R. Br.), might explain the disappearance of *P. n. oleracea* from part of its range and the concomitant establishment of *P. rapae*.

Recently, Benson *et al.* (2003b) argued against Chew's bottom-up hypothesis, suggesting that *P. n. oleracea* could have persisted on meadow crucifers that would have remained abundant after woodlands were cut. Benson *et al.* (2003b) offered a third hypothesis: that *P. n. oleracea*'s decline in the north-eastern United States was from top-down forces caused by a braconid parasitoid, *Cotesia glomerata* L., introduced to North America in the 1880s as a biological control agent for the agricultural pest *P. rapae*, an agricultural pest (Clausen 1978) with which it possibly coinvasion (Scudder 1889). In regions where *P. n. oleracea* populations declined, the butterflies have a second generation rather than enter diapause after the first generation, thus increasing exposure to the parasitoid (second generation parasitism rates = 30–100%), which has low numbers early in the season (Benson *et al.* 2003b; Van Driesche *et al.* 2003; Van Driesche, Nunn & Pasquale 2004).

We offer an alternative hypothesis to explain the loss of *P. n. oleracea* populations through bottom-up effects caused by an introduced weed, garlic mustard (*Alliaria petiolata* [Bieb.] Cavara & Grande). Garlic mustard was introduced from Europe to north-eastern North America in 1868 (Nuzzo 1993) and has spread to much of the native range of *P. n. oleracea* (Klots 1951; Opler

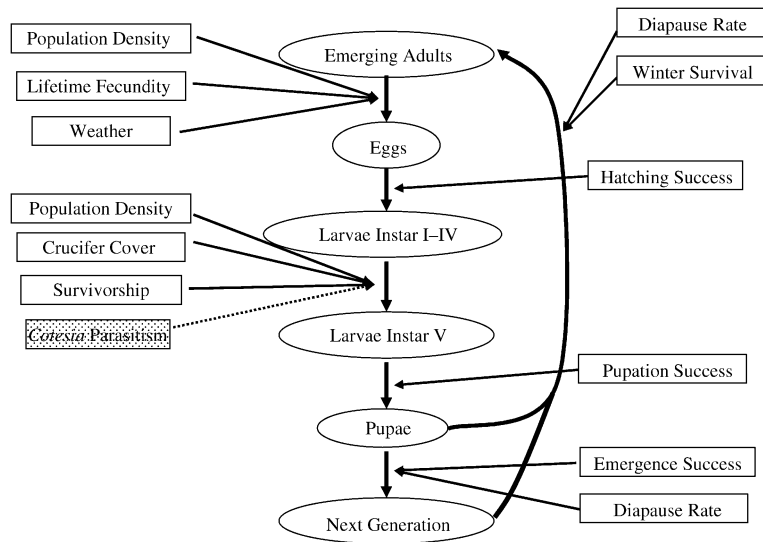
*et al.* 1984). The impact of *A. petiolata* on native plant and animal populations is relatively unknown, but it is widely assumed that *A. petiolata* displaces native understorey plants because invaded sites frequently have low native species-richness and cover (White, Haber & Keddy 1993; Anderson, Kelley & Dhillion 1996; McCarthy 1997). *P. n. oleracea* females oviposit on garlic mustard, but this plant does not support larval development (Courant *et al.* 1994; Huang, Renwick & Chew 1995). Oviposition on garlic mustard by *P. n. oleracea* is attributed to chemical similarities between it and native host plants (Feeny & Rosenberry 1982; Huang *et al.* 1995; Renwick 2002). Displacement or replacement (after habitat disturbance) of native plants by garlic mustard could have created a population sink and thus led to the decline of *P. n. oleracea*.

We created a stochastic simulation model of *P. n. oleracea* populations designed to test the relative strength of the alternative hypotheses for the decline of *P. n. oleracea* in the north-eastern United States, and to compare the potential importance of bottom-up and top-down forces in the decline. Using this model, we also evaluated two additional aspects of *P. n. oleracea* ecology: the potential importance of an infrequent third generation (Opler *et al.* 1984) to population recovery, and evolutionary pressure towards univoltinism, which would provide escape from *C. glomerata* parasitism (cf. Benson *et al.* 2003a).

## Materials and methods

### BIOLOGY OF *P. N. OLERACEA*

*P. n. oleracea* is generally bivoltine, with the first adults emerging between late April and early May, depending on location (Opler *et al.* 1984). Females begin laying eggs 3 days after emergence and can lay for approximately 2 weeks. First-generation adults are usually restricted to moist deciduous woodlands and swamps, where females lay eggs on the leaves of *C. diphylla* and other spring crucifers (Chew 1981), as well as on garlic mustard rosettes and bolting plants when present in the understorey (Courant *et al.* 1994). Eggs hatch in 5–7 days and larvae develop through five instars on the food plant selected by the mother. Although eggs are typically laid singly, females do not avoid ovipositing on plants on which eggs already have been laid. When two or more larvae develop on the same plant larvae leave the plant during the fourth or fifth instar, after depleting the food source, and seek another plant (Courtney & Courtney 1982; Chew, unpublished data). Parasitism does not usually affect the first generation because *C. glomerata* populations are low in May and June due to over-winter mortality (Shapiro 1981; Benson *et al.* 2003a). However, *C. glomerata* become abundant during the second *P. n. oleracea* generation (Benson *et al.* 2003a; Benson *et al.* 2003b). Pupae develop into adults within 7 days or enter pupal diapause, and emerge as adults the following spring. Diapause is highly labile,



**Fig. 1.** The life cycle of one generation of *P. n. oleracea*. Ovals depict life stages represented in the model, while rectangles indicate life-history and community parameters contributing to the transition between each stage. Parasitism by *C. glomerata* is shaded to indicate that it is a factor in only the second generation of each year.

and *Pieris* populations possess significant genetic variability for this trait (Lees & Archer 1981; Wiklund 1992; Courant & Chew 1995). The second generation hatches in July and moves from forests to open fields, where there are wild crucifers such as *Barbarea orthoceras* Ledeb., *Brassica rapa* L., *Sisymbrium officinale* L. and garlic mustard, as well as a diversity of cultivated varieties of *Brassica oleracea* L. (Chew 1981; Van Driesche *et al.* 2004). The second generation develops similarly to the first, but most pupae from the second generation enter diapause. A partial third generation is sometimes seen in September, when there are sufficient host plants and favourable environmental conditions (Chew 1981; Opler *et al.* 1984); because it is uncommon, this generation was not part of our baseline model.

#### MODEL STRUCTURE

A stochastic simulation model of a two-generation annual life cycle (Fig. 1) was created using STELLA software (version 8, iSee systems, Inc., New Hampshire, USA). Parameter values were based on our own and published empirical data. Insufficient data on *P. n. oleracea* were available for all parameters, so when needed, data from other subspecies of *P. napi* and occasionally from other *Pieris* species were used. Measures of variance were taken from empirical data when available; if distributional data were unavailable, a normal distribution with a standard deviation of 10% was assumed. The sensitivity of the model results to this assumption was tested as part of the analyses. Because of variability among studies in details of data collection and reporting, baseline parameter values are not summarized easily in a table. Therefore, each parameter is discussed below.

Only the female population was modelled, and each year started with emergence of females during the first

generation. The number of eggs laid ( $E$ ) in each generation was a function of the number of females emerging ( $N_i$ ), proportion of females not emigrating ( $F$ ), number of female eggs produced per female during a lifetime ( $E_f$ ) and proportion of days suitable for oviposition during the female's lifetime ( $D$ ):

$$E = N_i * F * E_f * D \quad \text{eqn 1}$$

Because temperature and solar radiation limit oviposition (Gossard & Jones 1977; Yamamoto & Ohtani 1979),  $D$  for each generation was calculated from 8 years (1996–2004) of hourly climate data from a site in the western portion of the simulated study area (North Adams, MA, USA; 42°42' N, 73°10' W) (NCDC 2005). Days were considered suitable for oviposition if the temperature was above 22 °C on overcast days (12–50% cloud cover) without precipitation, or above 18 °C with sun for 4+ hours between 10:00 and 16:00 (Cappuccino & Kareiva 1985; Chew unpublished data). If conditions were suitable for only 2–3 h, the day was considered as 0.5 days.  $D = 0.36 \pm 0.18$  for the first-generation flight period (1–21 May),  $0.73 \pm 0.11$  for the second generation (3 July–3 August), and when included in the model,  $0.62 \pm 0.06$  for the third generation (31 August–23 September).

Published values of lifetime fecundity ( $E_f$ ) of *P. napi* females differ. Yamamoto (1978) estimated that *P. n. nesis* lay 200–300 eggs (sexes combined) during their life span. Ohsaki (1982) found field-caged *P. n. nesis* females in northern Japan lay on average 228 eggs, whereas females in the wild lay 114. Wiklund *et al.* (1993) reported a mean lifetime fecundity of  $393.2 \pm 143.8$  for *P. n. napi* reared in greenhouses. Lifetime fecundity in the model was  $114 \pm 42$  female eggs, assuming a 1:1 sex ratio (Ohsaki 1982). The standard deviation was approximated from variation described by Wiklund *et al.* (1993).

We assumed that there were no Allee effects and that at low population densities all females stayed and bred ( $F=1$ ). However, as population density increased, females emigrated due to sexual encounters with males (Shapiro 1970). The density-dependent relationship between population size and females not emigrating was:

$$F = \left( P(0) - \left[ (P(0) - P(K_f)) \left( \frac{N}{K_f} \right)^B \right] \right) \quad \text{eqn 2}$$

Quantitative values for these parameters are not known, but a qualitative relationship has been observed (Chew, unpublished data). Consequently, the proportion of the population not emigrating when the population size is small,  $P(0)$  was set at 1.0, and the proportion not emigrating when adult population size was at carrying capacity,  $P(K_f)$ , was set at 0.6; the parameter determining steepness of decline ( $B$ ) as population size reached  $K_f$  was set at 8, to match qualitative observations. The initial number of females emerging in generation 1 of the first year was set arbitrarily at 3000 with  $K_f=100\,000$ .  $K_f$  was selected as an arbitrarily large number to represent the large, open population structure of *P. n. oleracea* (Chew 1981).

Number of first instar larvae ( $I_1$ ) was a function of  $E_f$  and hatching success ( $H$ ):

$$I_1 = E_f * H \quad \text{eqn 3}$$

$H$  was determined from field data and incorporated a number of external factors, such as predation, dislodgement and infertility, that might vary by generation.  $H = 0.73 \pm 0.073$  for generation 1 and  $0.53 \pm 0.053$  for generation 2, as reported by Yamamoto (1981a) for *P. n. nesis*. When a third generation was included in the model,  $H = 0.50 \pm 0.050$  (Yamamoto 1981b).

Survival from instar I to instar V during the first generation ( $I_{V1}$ ) was determined by survival rates on native crucifers ( $S_C$ ) and on garlic mustard ( $S_{GM}$ ), the proportion of the crucifer population that is garlic mustard ( $GM$ ), larval carrying capacity ( $K_L = 100\,000$ ), mean number of larvae per plant ( $\mu = I_1/K_L$ ) and the probability of a plant having more than one larva ( $\Omega$ ). Because of female oviposition behaviour, multiple eggs can be laid on a single plant by different females. Harcourt (1961) found larval distributions for *P. rapae*, which has a similar laying behaviour, were Poisson distributed during the first generation (eqn 4), and had a negative binomial distribution during generation 2 (eqn 5); the same was assumed in this model:

$$P(y) = \frac{\mu^y e^{-\mu}}{y!} \quad \text{eqn 4}$$

$$P(y) = \frac{(k+y-1)!}{y!(k-1)!} \left( \frac{\mu}{k+\mu} \right)^y \left( \frac{k}{k+\mu} \right)^k \quad \text{eqn 5}$$

In both equations  $P(y)$  was the probability that a plant contains  $y$  larvae, and  $\mu$  equalled the mean number of

larvae. *P. n. oleracea* females do not appear to discriminate during oviposition between garlic mustard and native crucifers (Huang *et al.* 1995; Keeler 2005), so it was assumed that there was an equal probability of all plants being selected for oviposition. Harcourt's (1961) estimate of 2.91 for *P. rapae* for the clumping factor  $k$  was used for the negative binomial distribution. The probability of a plant having more than one larva ( $\Omega$ ), therefore, was  $[1 - P(0) - P(1)]$ . Assuming that all larvae sharing host plants leave and either resettle on a native crucifer or die, the probability of resettling was equal to the probability of finding an empty native host plant. This resulted in the number of larvae surviving to the fifth instar for the first generation as:

$$I_{V1} = I_{I1} - [I_{I1} * GM * (1 - S_{GM})] - [I_{I1} * (1 - GM) * (1 - S_C)] - [I_{I1} * (1 - GM) * S_C * \Omega] + [I_{I1} * (1 - GM) * S_C * \Omega * (1 - GM) * e^{-\mu}] \quad \text{eqn 6}$$

That is, the number of fifth instar larvae was equal to the number of instar I larvae minus the number of larvae that die on garlic mustard; minus typical deaths on native crucifers; minus those that survive typical deaths on native crucifers and then leave the plant due to co-occupancy; plus those that leave the plant and find an empty native host. Survival to the fifth instar during the second generation ( $I_{V2}$ ) was modified to include mortality from parasitism by *C. glomerata* ( $C$ ) and a negative binomial distribution of larvae on plants:

$$I_{V2} = I_{I2} - [I_{I2} * GM * (1 - S_{GM})] - [I_{I2} * (1 - GM) * (1 - S_C)] - [I_{I2} * (1 - GM) * S_C * C] - [I_{I2} * (1 - GM) * S_C * (1 - C) * \Omega] + \left[ I_{I2} * (1 - GM) * S_C * (1 - C) * \Omega * (1 - GM) * \left( \frac{k}{k + \mu} \right)^k \right] \quad \text{eqn 7}$$

Thus,  $I_{V2}$  was equal to the number of instar I larvae minus the number of larvae that die on garlic mustard; minus typical deaths on native crucifers; minus those that survive typical deaths on native crucifers that are parasitized by *C. glomerata*; minus those that survive on native crucifers and then leave the plant due to co-occupancy; plus those that leave the plant and find an empty native host. For the third generation, when included in the model, the first generation equation was modified to include *C. glomerata*.

The survival rate of  $0.388 \pm 0.17$  on native crucifers ( $S_C$ ) used in the model was estimated from *P. rapae* experiments in New York (USA) and included all sources of variation (e.g. predation, disease, poor weather) (Schmaedick & Shelton 1999). Survival rate estimates of *P. n. nesis* from Japan, which varied from 0.297 in generation 1–0.017 in generation 2 (Yamamoto 1981b) were not used because they included parasitism by *C. glomerata*, which was included as a separate parameter.

The survival rate of *P. n. oleracea* on garlic mustard ( $S_{GM}$ ) was set at zero because Bowden (1971) provided evidence that *P. n. oleracea* larvae are unable to complete

development on garlic mustard. In field cages, Courant (1996) found survival rates on bolting plants ranging from 0.081 to 0.095, and complete mortality on garlic mustard rosettes. In laboratory conditions, survival on bolting plants can be higher (0.27–0.42), but remains zero on rosettes (Courant *et al.* 1994; Courant 1996). However, development of *P. n. oleracea* appears to be partially weight-gated (Van der Reijden & Chew 1992), so larvae that develop on lower quality plants such as garlic mustard do so very slowly (Chew 1975; Courant *et al.* 1994; Keeler 2005). When subjected to predation and parasitism, slow-developing larvae have little chance of reaching pupation (e.g. Loader & Damman 1991).

Pupation success ( $U$ ) of instar  $V$  larvae ( $I_V$ ) determined the number of pupae ( $Pu$ ):

$$Pu = I_V * U \quad \text{eqn 8}$$

Pupation success integrated a number of causes of mortality during the fifth instar, including predation and disease. Yamamoto (1981a) reported a range in pupation success of *P. n. nesis* in the wild from 0.452 in the first generation to 0.034 and 0.097 in the second and third generations, respectively. However, success rates included mortality due to parasitism, which was modelled separately. Therefore, for this model,  $U = 0.83 \pm 0.083$ , based on laboratory studies of *P. n. oleracea* (Keeler unpublished data).

The number of emerging adult females in the second generation ( $N_2$ ) was a function of  $Pu$ , the proportion of pupae that enter diapause ( $O$ ) and emergence success ( $M$ ):

$$N_2 = Pu * (1 - O) * M \quad \text{eqn 9}$$

First-generation diapause rates vary depending on rearing conditions. Lees & Archer (1981) found diapause rates in *P. n. napi* of between 0.100 and 0.127 depending on the temperature at which larvae were reared. Van Driesche *et al.* (2004) observed diapause rates in *P. n. oleracea* from 0.15 to 0.90 depending on host plant and locality. The model used a diapause rate of  $0.83 \pm 0.083$  for generation 1, as reported by Van Driesche *et al.* (2004) for *P. n. oleracea* on the native host *C. diphylla* in the simulated study area; all generation 2 pupae entered diapause. Emergence success ( $M$ ) encompasses a number of factors (e.g. predation, parasitism, disease and desiccation) that lead to unsuccessful eclosion. Yamamoto (1981a) reported emergence success for *P. n. nesis* of 0.75 but did not state clearly how this rate was determined. Consequently,  $M$  was set to equal  $0.41 \pm 0.041$ , as calculated by Van Driesche *et al.* (2004) for *P. n. oleracea* in field trails near the simulated study area.

Pupae that do not develop directly enter diapause, overwinter and emerge the following spring. The number of females emerging the following year ( $N_1$ ) was determined by the number of pupae entering diapause during each generation and over-winter survival ( $S_W$ ):

$$N_{1,t+1} = S_W * (Pu_{1,t} * O_{1,t} + Pu_{2,t} * O_{2,t}) \quad \text{eqn 10}$$

Very little is known about over-winter survival in *P. napi*, therefore the model used  $S_W = 0.169 \pm 0.017$ , based on Moss's (1933) study of *P. brassicae*, and was the same for larvae in both generations.

#### MODEL RUNS AND SENSITIVITY ANALYSES

Baseline and alternative models were run over a period of 50 years for 1000 iterations of each scenario. Females emerging each spring ( $N_i$ ) were tracked and model scenarios were compared using three output variables: probability of persistence (i.e. percentage of runs with  $N_i > 0$  at 50 years), median year to extinction for populations that went extinct, and for populations that persisted 50 years mean population size at year 50. The model was first run with baseline values for each input variable. Sensitivity of the model to changes in parameter values was evaluated using perturbation analysis (e.g. Akcakaya *et al.* 2003) by re-running the model repeatedly while varying one parameter at a time and keeping other parameters at baseline values. The goal was to establish which parameters are most likely to be important in determining *P. n. oleracea* persistence and abundance, and to identify parameters that need to be studied more thoroughly. Parameters were varied by increasing and decreasing mean values by 1 SD when empirical data were available for the standard deviation or by 10% when data were not available. Standard deviations were held constant across scenarios for those values calculated from empirical data and altered to maintain the assumed 10% variance for other parameters. Adult female population size in the baseline model never exceeded  $0.25 K_f$ , so the density-dependent emigration function was unimportant in the model outcome. Consequently, we did not assess sensitivity to  $K_f$ .

An additional scenario was run (1) to explore the importance of the magnitude of the assumed variances by separately changing the variance from 10% to 5% or 20% for each parameter for which variance could not be determined from empirical data. The model was also used to test hypotheses about the likelihood of bottom-up vs. top-down explanations of *P. n. oleracea* decline. Specifically, the model determined how population persistence changed with (2) increasing cover of garlic mustard, (3) increasing parasitism rates by *C. glomerata* and (4) the interaction between parasitism and garlic mustard cover. The effect of garlic mustard invasion was assessed by increasing the garlic mustard cover in 10% intervals until there was zero probability of persistence, while holding all other parameters at baseline values. The impact of parasitism by *C. glomerata* was determined by increasing mortality due to parasitism during the second generation in a similar manner. The interactive effects of garlic mustard invasion and increased parasitism by *C. glomerata* were examined by simultaneously altering the proportion of host plant that was garlic mustard and the mortality due to parasitism.

Finally, scenarios were generated to assess (5) the selective pressure on evolution towards univoltinism with increased parasitism by concurrently adjusting the diapause rate during the first generation and mortality due to parasitism during the second generation and (6) the potential importance of occasional third-generation to population recovery. A third generation was added in a probabilistic fashion to the baseline model as a condition of weather during the first and second generations. If  $D_1 > 0.409$  and  $D_2 > 0.76$ , then diapause during the second generation was  $O_2 = 0.91 \pm 0.091$ , else  $O_2 = 1.00$ . The effect of an occasional third generation under *C. glomerata* parasitism also was assessed by simultaneously adding in an occasional third generation using the method just described and increasing mortality incrementally due to parasitism during the second and third generations by 10%.

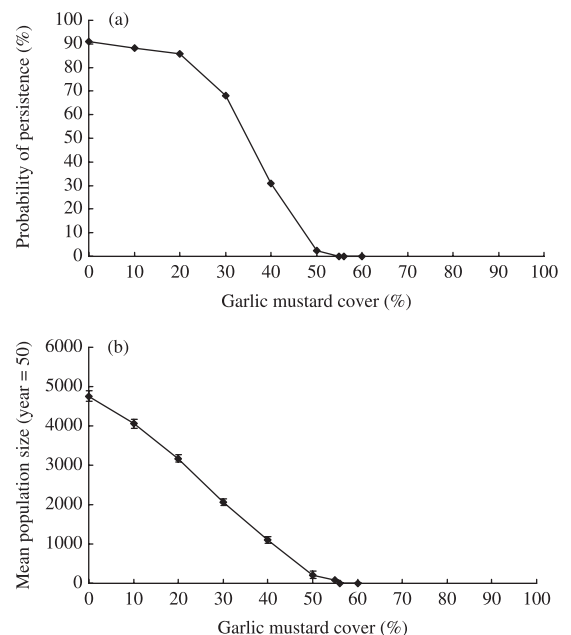
## Results

The baseline model predicted that simulated *P. n. oleracea* populations had a 90.8% probability of persisting for 50 years (Table 1). For populations that persisted, there was a mean population size of 4754 females (SD = 4003) at year 50, which is well below the modelled carrying capacity ( $K_j = 100\,000$ ). For populations that went extinct, median time to extinction was 22 years (Q-range = 24.5). Sensitivity analyses indicated that model results are robust to most single-parameter modifications. Modelled alterations of initial population size, hatching success, pupation success, emergence success and overwinter survival did not change the results appreciably relative to baseline (Table 1). Similarly, adjusting the variance assumed for some life-history parameters to 5% or 20% from the baseline of 10% caused only a slight change in probability of persistence (= 0.2–3.0%) or mean size of populations persisting to year 50 (= 0.2–6.1%).

However, when larval carrying capacity ( $K_L$ ) was decreased by one order of magnitude, the probability of persistence decreased by 51% and mean population size at year 50 for populations that persisted decreased by almost 90%. Median year to extinction declined to 1 year (Q-range = 13) for the low larval carrying capacity scenario but varied little for any other single parameter modification (Table 1). A twofold increase in larval carrying capacity did not alter the persistence probability substantially but did cause a 105% increase in mean population size. Mean population size changed consistently with changes in carrying capacity, staying at approximately 5% of  $K_L$  (Table 1). Reducing lifetime fecundity ( $E_f$ ) by 1 SD (37%) resulted in an approximately 50% decrease in persistence probability and mean population size. The model was also sensitive to a decrease in the number of days suitable for oviposition during generation 1 ( $D_1$ ) but not to any other modifications of this parameter in either generation. When larval survivorship on crucifers ( $S_C$ ) was lowered 1 SD (43%), persistence probability was reduced by 45% and

mean population size declined 43% (Table 1). Increasing  $S_C$  by 1 SD did not change the probability of persistence appreciably but did increase the mean population size by almost 60%. The model was sensitive to large changes in diapause rate during the first generation ( $O_1$ ). When  $O_1$  was changed from  $0.83 \pm 0.083$  to  $0.23 \pm 0.023$  the mean population size increased by 23%, but probability of persistence increased only slightly. When the population was made univoltine ( $O_1 = 1$ ) under baseline conditions, persistence probability declined by 16% and mean population size at year 50 was halved. Although immigration did not change mean population size considerably, immigration of even a single female during the second generation prevented the population from ever going extinct (Table 1).

Changes in garlic mustard cover (*GM*) and death rate due to parasitism by *C. glomerata* (*C*) exhibited threshold patterns in population persistence. As the proportion of crucifer cover that was garlic mustard was increased from 20% to 50%, the probability of population persistence decreased from 85.7% to 2.5% and persistence dropped to zero at  $GM = 56\%$  (Fig. 2a). For populations that persisted for 50 years, mean size started to decline at  $GM = 10\%$  (Fig. 2b). As parasitism by *C. glomerata* in the second generation was increased from 60% to 90%, the probability of persistence fell from 88.5% to 60.8% (Fig. 3a). However, even when all second-generation larvae were parasitized ( $C = 100\%$ ), there was still a 39.5% probability of the population persisting. This result occurred despite mean population size for populations persisting beginning to decline at  $C = 10\%$  (Fig. 3b). When moderate (50%) and high (90%) rates



**Fig. 2.** (a) Probability of persistence for 50 years ( $n = 1000$  model runs) and (b) mean population size ( $\pm 1$  SE) at 50 years for different values of garlic mustard cover. Mean population size was calculated only for model runs that persisted to year 50. Sample size for mean population is largest for zero garlic mustard ( $n = 908$ ) and declines as garlic mustard cover increases.

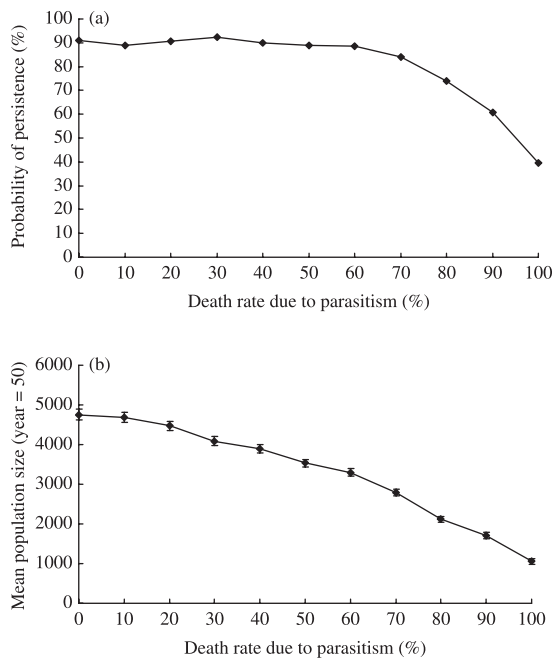
**Table 1.** Probability of persistence, mean population size at year 50 and median year to extinction for baseline models and alternative model scenarios that are single-parameter modifications of the baseline model. For each scenario, the baseline parameter value is given in brackets and the alternative scenario values are given in parenthesis. For population persistence and mean population size at year 50, the difference from baseline is given. Population size at year 50 includes only those population runs that persisted the entire 50 years

Scenario	Probability of persistence (%) ( $n = 1000$ runs)	Difference from baseline	Mean population size year 50 (SD)	% Difference from baseline	$n^a$	Median year to extinction (Q-range <sup>b</sup> )	$n^c$
Baseline	90.8	–	4754 (4003)	–	908	22 (24.5)	92
Initial number of females, $N_1$ (3000)							
Low (500)	90.0	–0.8	4737 (3882)	–0.36	900	25 (27.5)	100
High (6000)	90.4	–0.4	4902 (4036)	3.11	904	25 (26)	96
Carrying capacity, $K_L$ (100 000)							
Low (10 000)	40.1	–50.7	518 (401)	–89.10	401	1 (13)	599
High (200 000)	94.0	3.2	9754 (8058)	105.2	940	31.5 (23)	60
Lifetime fecundity, $E_f$ (114 ± 42)							
Low (72 ± 42)	33.7	–57.1	2122 (2879)	–55.36	337	23 (20)	663
High (156 ± 42)	79.6	–11.2	5349 (4252)	12.52	796	23 (25.5)	204
Days suitable for oviposition, generation 1, $D_1$ (0.36 ± 0.18)							
Low (0.18 ± 0.18)	45.3	–45.5	2694 (3416)	–43.33	453	24 (20)	547
High (0.54 ± 0.18)	83.8	–7.0	4984 (4064)	4.84	838	26.5 (29)	162
Days suitable for oviposition, generation 2, $D_2$ (0.73 ± 0.11)							
Low (0.62 ± 0.11)	90.4	–0.4	4410 (3722)	–7.24	904	25.5 (25)	96
High (0.84 ± 0.11)	90.5	–0.3	4967 (4004)	4.48	905	23 (21)	95
Hatching generation 1, $H_1$ (0.73 ± 0.073)							
Low (0.66 ± 0.066)	89.9	–0.9	4629 (3949)	–2.63	899	25 (24)	101
High (0.80 ± 0.080)	89.0	–1.8	4874 (4108)	2.52	890	21 (25)	110
Hatching generation 2, $H_2$ (0.53 ± 0.053)							
Low (0.48 ± 0.048)	88.4	–2.4	4596 (3860)	–3.32	884	27 (25.5)	116
High (0.58 ± 0.058)	89.5	–1.3	5010 (4065)	5.38	895	27 (22)	105
Larval survival, crucifers, $S_C$ (0.388 ± 0.17)							
Low (0.218 ± 0.17)	18.6	–72.2	1261 (1885)	–73.47	186	21 (18)	814
High (0.558 ± 0.17)	83.0	–7.8	7584 (5543)	59.53	830	27 (25)	170
Pupation success, $U$ (0.83 ± 0.083)							
Low (0.75 ± 0.075)	89.6	–1.2	4190 (3359)	–11.86	896	31 (23)	104
High (0.91 ± 0.091)	88.4	–2.4	5294 (4274)	11.36	884	27.5 (27)	116
Emergence success, $M$ (0.41 ± 0.041)							
Low (0.37 ± 0.037)	88.5	–2.3	4674 (3912)	–1.68	885	29 (20)	115
High (0.45 ± 0.045)	91.0	0.2	5191 (4124)	9.19	910	28.5 (26)	90
Diapause generation 1, $O_1$ (0.83 ± 0.083)							
Extreme low (0.23 ± 0.023)	98.6	7.8	5866 (3125)	23.39	986	25.5 (20)	14
Low (0.75 ± 0.075)	91.1	0.3	5273 (4183)	10.92	911	24 (23)	89
High (0.91 ± 0.091)	87.6	–3.2	4093 (3580)	–13.90	876	27 (19)	124
Survivorship winter, $S_W$ (0.169 ± 0.017)							
Low (0.152 ± 0.015)	90.9	0.1	4261 (3594)	–10.37	909	22 (22)	91
High (0.186 ± 0.019)	88.3	–2.5	5295 (4230)	11.38	883	27 (22)	117
Number of immigrants, generation 2 (0)							
1	100.0	9.2	4822 (4128)	1.43	1000	–	–
2	100.0	9.2	4775 (3951)	0.44	1000	–	–
5	100.0	9.2	4928 (3964)	3.66	1000	–	–
Univoltine ( $O_1 = 1.00$ )	74.9	–15.9	2054 (2252)	–56.79	749	29 (21)	251
Occasional trivoltine ( $O_2 = 0.91 ± 0.091$ )	88.4	–2.4	4754 (3977)	0	884	26.5 (25)	116
100% Trivoltine ( $O_2 = 0.91 ± 0.091$ )	84.2	–6.6	5865 (5073)	23.37	842	25 (21)	158

<sup>a</sup>Number of runs where population persisted 50 years; <sup>b</sup>difference between the upper and lower quartiles; <sup>c</sup>number of runs where population went extinct.

of parasitism were added to garlic mustard scenarios (ranging from 10% to 60% cover), the extinction threshold observed for changes in garlic mustard cover alone was eliminated (Fig. 4a) and persistence probability dropped sharply with increased parasitism. The combined effects of garlic mustard and parasitism also caused a more rapid decline of the mean size of persisting populations than with either effect alone (Fig. 4b).

Increased second-generation parasitism might favour selection for first-generation larvae to enter diapause, thereby becoming univoltine. Our model indicated that increased diapause rates during the first generation increased the probability of populations persisting only at parasitism rates  $\geq 70\%$  (Fig. 5a). The mean size of populations that persisted for 50 years was also larger for increased diapause rates, but only when parasitism

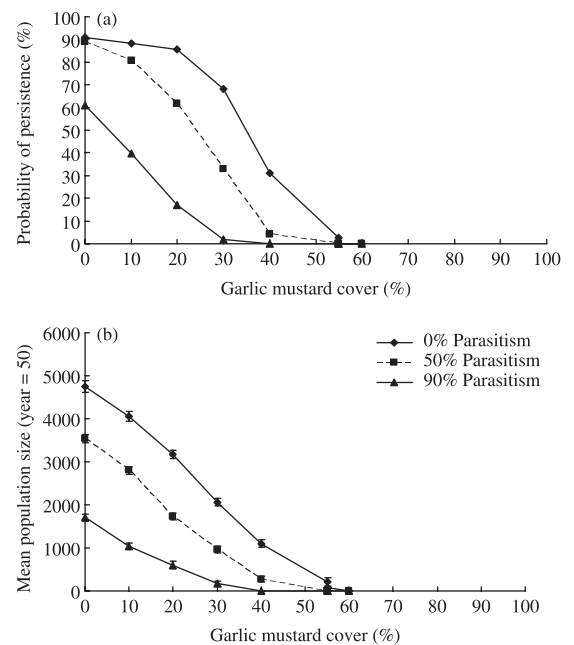


**Fig. 3.** (a) Probability of persistence for 50 years ( $n = 1000$  model runs) and (b) mean population size ( $\pm 1$  SE) at 50 years for varying death rates due to parasitism by *C. glomerata* in the second generation. Mean population size was calculated only for model runs that persisted to year 50. Sample size for mean population is largest for zero parasitism ( $n = 908$ ) and declines as death rate due to *C. glomerata* parasitism increases.

was above 60% (Fig. 5b). Addition of a third generation to approximately 15% of the model runs did not alter probability of persistence or mean population size appreciably under baseline conditions (Table 1). Increasing the frequency of trivoltine years to 100% also had little effect on persistence probability, but did increase mean population size by approximately 23% under baseline conditions (Table 1). Including an occasional third generation and parasitism, however, had virtually no effect on the probability of populations persisting or on mean population size ( $r^2 = 0.99$  between model results with and without a third generation for both output measures).

### Discussion

Results of our model indicate that under baseline conditions population dynamics of *P. n. oleracea* are dictated primarily by larval carrying capacity, reproduction, larval survivorship, immigration and diapause rate. Other model parameters were of only intermediate or low sensitivity, and our analyses indicated that these results are robust to single-parameter inaccuracies in parameter and variance estimates. We found that decreasing larval carrying capacity, expressed as the number of plants available for oviposition and larval development, led to a sharp decline in the probability of population persistence and to smaller population sizes for populations that persisted. In combination with egg distribution patterns across plants, larval carrying

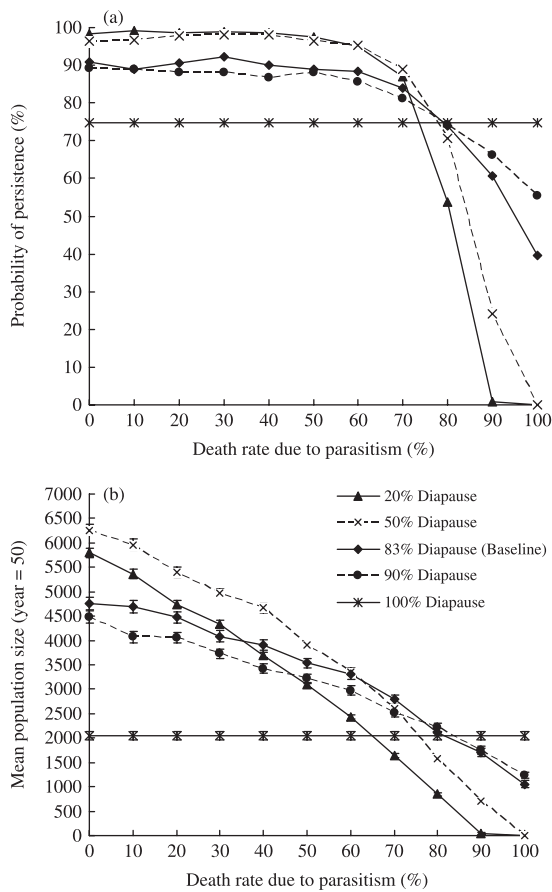


**Fig. 4.** (a) Probability of persistence for 50 years ( $n = 1000$  model runs) and (b) mean population size ( $\pm 1$  SE) at 50 years for interactions between garlic mustard and parasitism. Mean population size was calculated only for model runs that persisted to year 50. Sample size for mean population is largest for zero garlic mustard ( $n = 908$ ) and declines as garlic mustard cover and death rate due to *C. glomerata* parasitism increases.

capacity influenced density-dependent larval mortality associated with movement away from depleted food resources. Shapiro (1975) and Courtney & Courtney (1982) observed similar intraspecific larval competition in *P. napi* when egg distributions are clumped at low plant densities. Although it is difficult to quantify the carrying capacity of natural habitats (McNab 1985), we believe our model accurately reflects the role that resource limitation can have in determining *P. n. oleracea* population sizes (cf. Dempster & Pollard 1981). Reducing reproduction by decreasing lifetime fecundity or the number of days suitable for oviposition during the first generation caused a substantial decrease in persistence probability and mean population size. We believe that the model's sensitivity to the days suitable for oviposition is indicative of the importance of weather in limiting *P. n. oleracea* populations (cf. Gossard & Jones 1977).

Differences in larval survivorship on crucifers caused appreciable changes in population persistence and mean size of populations persisting to year 50. Larval survivorship ( $S_C$ ) incorporated factors such as predation, disease and poor climate conditions, and was estimated from studies of *P. rapae* near the simulated study area (Schmaedick & Shelton 1999). Decreasing  $S_C$  resulted in a decrease in both probability of persistence and mean population size. However, increasing  $S_C$  also caused a slight decrease in probability of population persistence despite a large increase in population size at year 50 for populations that persisted. These patterns reflect the





**Fig. 5.** (a) Probability of persistence for 50 years ( $n = 1000$  model runs) and (b) mean population size ( $\pm 1$  SE) at 50 years of model runs persisting for 50 years, for different combinations of rates of diapause and death due to parasitism by *C. glomerata*. Mean population size was calculated only for model runs that persisted to year 50. Sample sizes for figure (b) are largest for zero parasitism (20% diapause,  $n = 984$ ; 50% diapause,  $n = 963$ ; 83% diapause,  $n = 908$ ; 90% diapause,  $n = 891$ ; 100% diapause,  $n = 749$ ) and decline as death rate due to *C. glomerata* parasitism increases.

susceptibility of smaller model populations to stochastic events, and the increased influence of density-dependent mortality in larger populations. As expected from models of metapopulation rescue effects (Brown & Kodric-Brown 1977), we found immigration of females eliminated extinction under baseline conditions but did not notably alter the size of persisting populations. Data from translocations of *P. n. oleracea* suggest that the species is highly mobile, capable of moving more than 2 km, and recognize few if any barriers to movement (Chew 1981). In addition, Chew & Courtney (1991) noted that some Pierids establish persistent local populations where there are low-amplitude fluctuations in host plant numbers, while other populations are more ephemeral where host plant numbers fluctuate over orders of magnitude across years. These empirical observations, combined with our model results, suggest that over large spatial scales *P. n. oleracea* have a metapopulation structure where immigration is an important mechanism for metapopulation persistence.

Populations in our model were susceptible to changes in diapause rate during the first generation. In the absence of intense parasitism, persistence probability and mean population size were higher at low rates of first-generation diapause. When death rates due to parasitism by *C. glomerata* increased above 70%, however, higher rates of diapause increased the probability of population persistence. The addition of a third generation to baseline conditions or to *C. glomerata* scenarios did not enhance population persistence as predicted. It appears that although occasional third generations might contribute to individual fitness, they do not play a major role in population persistence of *P. n. oleracea* within the constraints of this model.

Model results indicate that when *C. glomerata* and garlic mustard are considered separately, bottom-up forces are more important in regulating abundance and persistence of *P. n. oleracea* populations. Simulated invasion by garlic mustard caused an acute decline in the probability of population persistence and appreciably smaller populations. The probability of persisting 50 years dropped to zero at 56% garlic mustard cover but never reached zero under any *C. glomerata* scenarios, even when mortality due to parasitism in the second generation was 100%. The impact of garlic mustard was exacerbated by *C. glomerata*. The threshold pattern on persistence relative to garlic mustard cover seen in garlic-mustard-only scenarios was lost, and populations had lower persistence probabilities for given amounts of garlic mustard. These trends can, for the most part, be explained by the fact that parasitism does not affect the first generation. *C. glomerata* populations are small during spring, and woodlands inhabited by the first generation *P. n. oleracea* are not suitable for the parasitoid (cf. Shapiro 1981; Benson *et al.* 2003a). Additionally, *P. n. oleracea* in our simulated study area have a high rate of diapause during the first generation (Van Driesche *et al.* 2004). Garlic mustard, in contrast, is present throughout the season in forests and along edges of fields and roads, as well as in open meadows (Cavers, Heagy & Kokron 1979; Nuzzo 1991, 1999; Dhillion & Anderson 1999).

Considering the historic decline of *P. n. oleracea* in the north-eastern United States, results from the reduced carrying capacity scenario are consistent with Chew's (1981) hypothesis that shifts in land use and understorey destruction, with its associated loss of native host plants, could have reduced *P. n. oleracea* populations. Benson *et al.*'s (2003b) argument against this bottom-up hypothesis, that *P. n. oleracea* would have been able to exist on meadow crucifers, ignored Chew's (1981) observation that there are no early spring meadow crucifers suitable for *P. n. oleracea* in its native range. *P. n. oleracea* is currently abundant in northern Vermont compared to western Massachusetts (our simulated study area) (Benson *et al.* 2003b). Benson *et al.* (2003b) hypothesized that the difference in survival of populations of *P. n. oleracea* between the sites is due to avoidance of *C. glomerata* parasitism by differential diapause during

the first generation (being greater further north). The outcome of our model, of the interaction between parasitism and diapause, partly supports their hypothesis. However, our model predicted a moderate to high probability of population persistence (39.5–92.2%) for the diapause and parasitism rates reported by Van Driesche *et al.* (2003, 2004) and Benson *et al.* (2003b) in areas where *P. n. oleracea* populations have declined. In fact, our model predicted only a low persistence probability (< 25%) at diapause rates considerably lower than those reported for *P. n. oleracea* on its native host plant (Van Driesche *et al.* 2004). Therefore, it seems unlikely that top-down forces alone, from the invasion of *C. glomerata* and differential diapause rates, are sufficient to explain the local persistence of some populations of *P. n. oleracea* and the decline of others.

In summary, we propose an explanation of *P. n. oleracea* decline that favours bottom-up forces, but incorporates both Chew's and Benson *et al.*'s hypotheses. Garlic mustard invaded Massachusetts during the 1930–40s and southern Vermont in the 1970–80s, and is currently abundant throughout Massachusetts but remains absent from central and northern Vermont (Nuzzo 1993; Drayton 2001; USDA 2004). Research has shown that after garlic mustard invades a forest it becomes a permanent part of the community, spreading an average > 5 m per year even in relatively undisturbed habitat (Nuzzo 1999). Although there are no data currently available on the relative abundance of garlic mustard compared to native crucifers in areas where it has invaded, estimates of garlic mustard cover relative to all understorey plant species range from 6% to 60% (McCarthy 1997; Nuzzo 1999; Stinson *et al.* in review). At high densities of garlic mustard, our model predicts a low probability of *P. n. oleracea* persistence. Therefore, garlic mustard invasion alone could explain local declines of *P. n. oleracea*. However, garlic mustard invasion could also exacerbate the effects of both habitat loss and larval parasitism by *C. glomerata*, which has invaded entire native ranges of *P. n. oleracea* (Benson *et al.* 2003b). Consequently, we suggest that the effects of forest and native plant loss, combined with consecutive invasions by *C. glomerata* and garlic mustard, interacted to reduce *P. n. oleracea* populations. A host plant and parasitism interaction hypothesis was proposed and dismissed by Benson *et al.* (2003b), but they were considering host plant limitation due to land use rather than by an invasive plant. Based on our modelling, however, we view this as a probable scenario, with garlic mustard invasion and bottom-up forces being the primary factors driving population decline.

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### References

- Akcakaya, H.R., Atwood, J.L., Breininger, D., Collins, C.T. & Duncan, B. (2003) Metapopulation dynamics of the California least tern. *Journal of Wildlife Management*, **67**, 829–842.
- Anderson, R.C., Kelley, T.C. & Dhillion, S.S. (1996) Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*) in central Illinois. *Restoration Ecology*, **4**, 181–191.
- Benson, J., Pasquale, A., Van Driesche, R.G. & Elkinton, J. (2003a) Assessment of risk posed by introduced braconid wasps to *Pieris virginiensis* a native butterfly in New England. *Biological Control*, **26**, 83–93.
- Benson, J., Van Driesche, R.G., Pasquale, A. & Elkinton, J. (2003b) Introduced braconid parasitoids and range reduction of a native butterfly in New England. *Biological Control*, **28**, 197–213.
- Bowden, S.R. (1971) American white butterflies (Pieridae) and English food-plants. *Journal of the Lepidopterists' Society*, **25**, 6–12.
- Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology*, **58**, 445–449.
- Cappuccino, N. & Kareiva, P. (1985) Coping with a capricious environment: a population study of a rare Pierid butterfly. *Ecology*, **66**, 152–161.
- Cavers, P.B., Heagy, M.I. & Kokron, R.F. (1979) The biology of Canadian weeds. 35. *Alliaria petiolata* (M.Bieb.) Cavara and Grande. *Canadian Journal of Plant Science*, **59**, 217–229.
- Chew, F.S. (1975) Coevolution of Pierid butterflies and their cruciferous foodplants I. The relative quality of available resources. *Oecologia*, **20**, 117–127.
- Chew, F.S. (1981) Coexistence and local extinction in two Pierid butterflies. *American Naturalist*, **118**, 655–672.
- Chew, F.S. & Courtney, S. (1991) Plant apparency and evolutionary escape from insect herbivory. *American Naturalist*, **138**, 729–750.
- Clausen, C.P. (1978) *Introduced Parasites and Predators of Arthropod Pests and Weeds: a World Review*. USDA, Washington.
- Courant, A.V. (1996) The effect of a naturalized crucifer on the feeding ecology of *Pieris napi oleracea* and *Pieris virginiensis* (Lepidoptera: Pieridae). Master's thesis, Tufts University, Medford.
- Courant, A.V. & Chew, F.S. (1995) Latent polymorphism and direct development in *Pieris virginiensis* (Pieridae). *Journal of the Lepidopterists' Society*, **49**, 84–87.
- Courant, A.V., Holbrook, A.E., Van der Reijden, E.D. & Chew, F.S. (1994) Native Pierine butterfly (Pieridae) adapting to naturalized crucifer. *Journal of the Lepidopterists' Society*, **48**, 168–170.
- Courtney, S.P. & Courtney, S. (1982) The 'edge-effect' butterfly oviposition: causality in *Anthocharis cardamines* and related species. *Ecological Entomology*, **7**, 131–137.
- Dawes-Gromadzki, T. (2002) Trophic trickles rather than cascades: conditional top-down and bottom-up dynamics in an Australian chenopod shrubland. *Austral Ecology*, **27**, 490–508.
- Dempster, J.P. & Pollard, E. (1981) Fluctuations in resource availability and insect populations. *Oecologia*, **50**, 412–416.
- Dhillion, S.S. & Anderson, R.C. (1999) Growth and photosynthetic response of first-year garlic mustard (*Alliaria petiolata*) to varied irradiance. *Journal of the Torrey Botanical Society*, **126**, 9–14.
- Drayton, B. (2001) A new Record for *Alliaria petiolata* (Brassicaceae) in Hillsborough County, New Hampshire. *Rhodora*, **103**, 323–325.

- Feeny, P. & Rosenberry, L. (1982) Seasonal-variation in the glucosinolate content of North-American *Brassica nigra* and *Dentaria* species. *Biochemical Systematics and Ecology*, **10**, 23–32.
- Gossard, T.W. & Jones, R.E. (1977) The effects of age and weather on egg laying in *Pieris rapae* (L.). *Journal of Applied Ecology*, **14**, 65–71.
- Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control and competition. *American Naturalist*, **44**, 421–425.
- Harcourt, D.G. (1961) Spatial pattern of the imported cabbage-worm, *Pieris rapae* (L.) (Lepidoptera: Pieridae), on cultivated Cruciferae. *Canadian Entomologist*, **93**, 945–952.
- Harrison, S. & Cappuccino, N. (1995) Using density-manipulation experiments to study population regulation. In: *Population Dynamics: New Approaches and Synthesis* (eds N. Cappuccino & P.W. Price), pp. 131–148. Academic Press, San Diego.
- Huang, X.P., Renwick, J.A.A. & Chew, F.S. (1995) Oviposition stimulants and deterrents control acceptance of *Alliaria petiolata* by *Pieris rapae* and *P. napi oleracea*. *Chemoecology*, **5**, 79–87.
- Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724–732.
- Hunter, M.D., Varley, G.C. & Gradwell, G.R. (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences*, **94**, 9176–9181.
- Jiang, L. & Morin, P.J. (2005) Predator diet breadth influences the relative importance of bottom-up and top-down control of prey biomass and diversity. *American Naturalist*, **165**, 350–363.
- Keeler, M.S. (2005) *Interactions Between a Native Butterfly and Multiple Exotic Species: Consequences and Prospects*. Master's thesis, Tufts University, Medford.
- Klots, A.B. (1951) *A Field Guide to the Butterflies of North America East of the Great Plains* Houghton Mifflin, Boston.
- Lees, E. & Archer, D.M. (1981) Diapause in various populations of *Pieris napi* L. from different parts of the British Isles. *Journal of Research on the Lepidoptera*, **19**, 96–100.
- Loader, C. & Damman, H. (1991) Nitrogen content of food plants and vulnerability of *Pieris rapae* to natural enemies. *Ecology*, **72**, 1586–1590.
- Longstaff, G.B. (1912) *Butterfly-Hunting in Many Lands*. Longmans and Green, London.
- McCarthy, B.C. (1997) Response of a forest understorey community to experimental removal of an invasive non-indigenous plant (*Alliaria petiolata*, Brassicaceae). *Assessment and Management of Plant Invasions* (eds J.O. Luken & J.W. Thieret), pp. 117–130. Springer-Verlag, New York.
- McNab, J. (1985) Carrying capacity and related slippery shibboleths. *Wildlife Society Bulletin*, **13**, 403–410.
- Mooney, H.A. & Cleland, E.E. (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, **98**, 5446–5451.
- Moss, J.E. (1933) The natural control of the cabbage caterpillars, *Pieris* spp. *Journal of Animal Ecology*, **2**, 210–231.
- Murdoch, W.W. (1966) Community structure, population control, and competition – a critique. *American Naturalist*, **100**, 219–226.
- NCDC (2005) *Unedited Local Climatological Data, 2005*. NOAA.
- Nuzzo, V. (1991) Experimental control of garlic mustard *Alliaria petiolata* [(Bieb.) Cavara & Grande] in northern Illinois using fire, herbicide and cutting. *Natural Areas Journal*, **11**, 158–167.
- Nuzzo, V. (1993) Distribution and spread of the invasive biennial *Alliaria petiolata* (garlic mustard) in North America. *Biology Pollution, the Control and Impact of Invasive Exotic Species* (ed. B.N. McKnight), pp. 137–145. Indiana Academy of Sciences, Indianapolis.
- Nuzzo, V. (1999) Invasion pattern of the herb garlic mustard (*Alliaria petiolata*) in high quality forests. *Biological Invasions*, **1**, 169–179.
- Ohsaki, N. (1982) Comparative population studies of three *Pieris* butterflies, *P. apae*, *P. elete*, and *P. napi*, living in the same area III. Differences in the annual generation numbers in relation to habitat selection by adults. *Researches on Population Ecology (Tokyo)*, **24**, 193–210.
- Opler, P.A. & Krizek, G.O. (1984) *Butterflies East of the Great Plains* Johns Hopkins University Press, Baltimore.
- Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.
- Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology*, **73**, 733–746.
- Renwick, J.A.A. (2002) The chemical world of crucivores: lures, treats and traps. *Entomologia Experimentalis et Applicata*, **104**, 35–42.
- Schmaedick, M.A. & Shelton, A.M. (1999) Experimental evaluation of arthropod predation of *Pieris rapae* (Lepidoptera: Pieridae) eggs and larvae on cabbage. *Environmental Entomology*, **28**, 439–444.
- Schmitz, O.J., Hamback, P.A. & Beckerman, A.P. (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist*, **155**, 141–153.
- Scudder, S.H. (1889) *The Butterflies of the Eastern United States and Canada*. Houghton, Mifflin, Boston.
- Shapiro, A.M. (1970) The role of sexual behavior in density related dispersal of Pierid butterflies. *American Naturalist*, **104**, 367–373.
- Shapiro, A.M. (1975) Ecological and behavioral aspects of coexistence in six crucifer-feeding Pierid butterflies in the Central Sierra Nevada. *American Midland Naturalist*, **93**, 424–433.
- Shapiro, A.M. (1981) Susceptibility of *Pieris napi microstriata* (Pieridae) to *Apanteles glomeratus* (Hymenoptera: Braconidae). *Journal of the Lepidopterists Society*, **35**, 256.
- Simon, K.S. & Townsend, C.R. (2003) Impacts of freshwater invaders at different levels of ecological organization, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology*, **48**, 982–994.
- Stadler, B. (2004) Wedged between bottom-up and top-down processes: aphids on tansy. *Ecological Entomology*, **29**, 106–116.
- United States Department of Agriculture (USDA), NRCS (2004) *The PLANTS Database*, version 3.5 National Plant Data Center.
- Van der Reijden, E.D. & Chew, F.S. (1992) Assessing host-plant suitability in caterpillars: is the weight worth the wait? *Proceedings of the Eighth International Symposium on Insect-Plant Relationships* (eds S.B.J. Menken, J.H. Visser & P. Harrewijn), pp. 69–70. Kluwer Academic Publishing, Dordrecht.
- Van Driesche, R.G., Nunn, C., Kreke, N., Goldstein, B. & Benson, J. (2003) Laboratory and field host preferences of introduced *Cotesia* spp. parasitoids (Hymenoptera: Braconidae) between native and invasive *Pieris* butterflies. *Biological Control*, **28**, 214–221.
- Van Driesche, R.G., Nunn, C. & Pasquale, A. (2004) Life history pattern, host plants, and habitat as determinants of population survival of *Pieris napi oleracea* interacting with an introduced braconid parasitoid. *Biological Control*, **29**, 278–287.
- White, D.J., Haber, E. & Keddy, C. (1993) *Invasive Plants of Natural Habitats in Canada* (ed. Canadian Museum of Nature), pp. 121. Canadian Museum of Nature, Ottawa.
- Wiklund, C. (1992) A sex difference in the propensity to enter direct-diapause development: a result of selection for protandry. *Evolution*, **46**, 519–528.
- Wiklund, C., Kaitala, A., Virpi, L. & Abenius, J. (1993) Polyandry and its effect on female reproduction in the green-veined

- white butterfly (*Pieris napi* L.). *Behavioral Ecology and Sociobiology*, **33**, 25–33.
- Yamamoto, M. (1981a) Comparison of population dynamics of two Pierid butterflies, *Pieris rapae crucivora* and *P. napi nesis*, living in the same area and feeding on the same plant in Sapporo, Northern Japan. *Journal of the Faculty of Science, Series VI, Zoology Hokkaido University*, **22**, 202–249.
- Yamamoto, M. (1981b) Comparison of population dynamics of two Pierid butterflies, *Pieris rape crucivora* and *P. napi nesis*, living in the same area and feeding on the same plant in Sapporo Northern Japan. *Journal of the Faculty of Science Series VI. Zoology Hokkaido University*, **22**, 202–249.
- Yamamoto, M. & Ohtani, T. (1979) Number of eggs laid by *Pieris rapae crucivora*, compared with *P. napi nesis*, in Sapporo (Lepidoptera: Pieridae). *Kontyu*, **47**, 530–539.

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