

Differential Effects of Weather and Natural Enemies on Coexisting Aphid Populations

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ABSTRACT Study of mechanisms responsible for regulating populations of living organisms is essential for a better comprehension of the structure of biological communities and evolutionary forces in nature. Aphids (Hemiptera: Sternorrhyncha) comprise a large and economically important group of phytophagous insects distributed worldwide. Previous studies determined that density-dependent mechanisms play an important role in regulating their populations. However, only a few of those studies identified specific factors responsible for the observed regulation. Time series data used in this study originated from the untreated control plots that were a part of potato (*Solanum tuberosum* L.) insecticide trials in northern Maine from 1971 to 2004. The data set contained information on population densities of three potato-colonizing aphid species (buckthorn aphid, *Aphis nasturtii*; potato aphid, *Macrosiphum euphorbiae*; and green peach aphid, *Myzus persicae*) and their natural enemies. We used path analysis to explore effects of weather and natural enemies on the intrinsic growth rates of aphid populations. Weather factors considered in our analyses contributed to the regulation of aphid populations, either directly or through natural enemies. However, direct weather effects were in most cases detectable only at $P \leq 0.10$. Potato aphids were negatively affected by both fungal disease and predators, although buckthorn aphids were negatively affected by predators only. Parasitoids did not have a noticeable effect on the growth of any of the three aphid species. Growth of green peach aphid populations was negatively influenced by interspecific interactions with the other two aphid species. Differential population regulation mechanisms detected in the current study might at least partially explain coexistence of three ecologically similar aphid species sharing the same host plant.

KEY WORDS population regulation, aphids, path analysis, coexistence

Study of mechanisms responsible for regulating populations of living organisms is essential for a better comprehension of the structure of biological communities and evolutionary forces in nature, making it one of the central areas of both theoretical and applied ecology (Pianka 1974, Berryman 1981, Emlen 1984, Turchin 1995). Historically, regulation mechanisms were broadly classified as being either density-dependent when average population growth rate depends to a certain degree on present and/or past population densities, or as density-independent in all other cases (Royama 1977, 1992; Hanski 1990; Turchin 1995). Predation and competition usually are held responsible for the density-dependent regulation, while unpredictable weather events and other abiotic disturbances are the driving force behind the density-independent regulation. For a considerable period of time, the two regulation types were considered to be mutually exclusive, and some authors questioned the existence of density-dependent regulation altogether (Hanski et al. 1993, Holyoak and Lawton 1993, Wolda

and Dennis 1993, Wolda et al. 1994). However, the current consensus is that both types exist and often act jointly. Furthermore, there is mounting theoretical and empirical evidence that a correct interpretation of population processes is impossible without knowing the relative contribution of density-dependent regulation and environmental stochasticity to their temporal dynamics (Sinclair and Pech 1996, Rothery et al. 1997, Lewellen and Vessey 1998, Nowicki et al. 2009).

Aphids (Hemiptera: Sternorrhyncha) comprise a large and economically important group of phytophagous insects distributed worldwide. Because many aphid species are highly damaging to cultivated plants, regulation of their populations has attracted a considerable amount of scientific attention. Populations of a few studied species appeared to be regulated by density-independent mechanisms (Holyoak and Lawton 1992, Woiwod and Hanski 1992, Wool 2002). However, both theoretical arguments (Dixon 1985) and analyses of field data (Wellings et al. 1985, Turchin and Taylor 1992, Woiwod and Hanski 1992, Maudsley et al. 1996, Sequeira and Dixon 1997, Jarošík and Dixon 1999, Alyokhin et al. 2005, Bommarco et al. 2007) suggest

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that density-dependent regulation is far more common. Although generating very useful information, none of those studies identified specific factors responsible for the observed effect. Aphids are commonly attacked by a complex of natural enemies that may dramatically reduce their populations (Dixon 2000, Hajek 2004, Hirose 2006). However, their relative contribution to the regulation of aphid populations over long periods of time is often unknown. Slosser et al. (1998) analyzed a 7-yr time series of the population density of the cotton aphid, *Aphis gossypii* Glover, on dryland cotton and found population dynamics are affected by complex interactions among temperature, solar irradiation, plant condition, and observed abundance of lady beetle adults and larvae (Coleoptera: Coccinellidae), lacewing larvae (Neuroptera: Chrysopidae), and hover fly larvae (Diptera: Syrphidae).

Buckthorn aphid, *Aphis nasturtii* Kaltenbach; potato aphid, *Macrosiphum euphorbiae* (Thomas); and green peach aphid, *Myzus persicae* (Sulzer) are three polyphagous species with essentially worldwide distribution (Blackman and Eastop 2000). All three species overwinter as eggs on wild hosts. In the spring, they undergo several parthenogenic wingless generations, and then produce parthenogenic winged spring migrants that leave winter hosts and colonize secondary summer hosts, including potato (*Solanum tuberosum* L.). Progeny of the spring migrants are also parthenogenic and usually wingless, although high aphid densities and deteriorating plant quality may lead to production of winged summer migrants. Several overlapping generations are produced during the summer. In the fall, short day photoperiod induces production of sexual fall migrants that return to the primary winter hosts (Radcliffe et al. 1993).

In a recent study, (Alyokhin et al. 2005) modeled density-dependent and -independent effects on population growth of the buckthorn aphid, potato aphid, and green peach aphid by using a 55-yr time series and found strong evidence of density-dependent regulation. In the current study, we further analyzed a subset of those data that, starting from 1971, was accompanied by natural enemy counts. Our approach in this study was not to establish whether density-dependent mechanisms exist as in our previous investigation (Alyokhin et al. 2005), but to elucidate the role of natural enemies in regulation of potato-colonizing aphid species. Although potato-colonizing aphids in northern Maine are affected by a diverse and abundant natural enemy complex (Shands et al. 1972a,b,c; Alyokhin and Sewell 2004), there is also evidence that their populations are primarily regulated by migration and density-independent weather factors (Shands and Simpson 1959, Shands et al. 1963). Better understanding of the driving forces behind observed fluctuations in aphid populations is likely to improve our ability to manipulate their densities in commercial potato production.

Materials and Methods

Aphid and Natural Enemy Population Data. Data used in this study originated from the untreated control plots that were a part of potato insecticide trials at the University of Maine Aroostook Research Farm, Presque Isle, ME. The trials were conducted every year between 1971 and 2004, with study protocols being very similar between the years. Experimental plots were 17.7 m long and four potato rows wide. The distance between the rows was ≈ 90 cm, and seed spacing was ≈ 35 cm. Approximately 1.8 m was left between the plots within each block, and blocks were spaced at ≈ 3 m. All plots were fertilized with N-P-K fertilizer at planting and sprayed weekly with fungicides to control fungal diseases of potatoes. Between five and 30 plots were planted each year, depending on the number of insecticide treatments tested. Potatoes were grown in a 3-yr rotation with clover (*Trifolium* spp.) and small grains.

Certified seed potato tubers were cut into 75–80-g pieces and planted at the experimental plots. All plots were planted to 'Katahdin' between 1971 and 1998 and in 2004. In 1999–2001, all plots were planted to transgenic New Leaf 'Atlantic' that expressed *Bacillus thuringiensis* subsp. *tenebrionis* Cry3A delta-endotoxin in its foliage. In 2002, five plots were planted to 'Katahdin', five plots to New Leaf 'Atlantic', and five plots to nontransgenic 'Atlantic.' In 2003, five plots were planted to nontransgenic 'Atlantic', and five plots were planted to New Leaf 'Atlantic.' When more than one cultivar was planted, their aphid population counts were averaged, weighting by proportion of each cultivar planted.

Aphid and natural enemy counts were based upon potato plant sampling from late June until late August between 1971 and 2004. Twenty-five plants were randomly selected in each plot at weekly intervals from the middle two rows of each plot. The number of plants sampled in each plot was reduced to 20 starting in 1995. One top, one middle, and one bottom leaf of each selected plant were randomly chosen for examination. Earlier studies (Shands et al. 1954) demonstrated that a three-leaf sampling method accurately estimated the number of aphids inhabiting the whole plant. The number of buckthorn aphids, potato aphids, green peach aphids, and natural enemies on each chosen leaf were counted. The natural enemies were identified and recorded as lady beetle (Coleoptera: Coccinellidae) adults, eggs, larvae, and pupae, spiders (Araneae), hover fly (Diptera: Syrphidae) eggs and larvae, green lacewing (Neuroptera: Chrysopidae) eggs and larvae, predaceous midge larvae (Diptera: Cecidomyiidae), aphids killed by fungi, and mummies of aphids parasitized by Hymenoptera. Lady beetle adults were the only natural enemies identified to species. (Shands et al. 1963, 1972a) who surveyed entomopathogenic fungi attacking aphids on Maine potatoes from 1952 to 1969 identified them as *Entomophthora thaxteriana* (the most abundant species responsible for 60–99% of the observed mortality), *E. aphidis*, *E. coronata*, *E. sphaerosperma*, *E. planchoni-*

ana, and *E. obscura* (Zygomycetes: Entomophthorales). A parasitoid survey was conducted from 1963 to 1967 and yielded at least 15 different species (Shands et al. 1972b), with *Aphidius nigripes* (Ashmead) and *Praon* spp. (Hymenoptera: Braconidae) being the most common ones. However, we do not know whether species composition of entomopathogenic fungi and parasitoids remained the same in the subsequent years. That was certainly not the case with lady beetles (Alyokhin and Sewell 2004).

Weather Data. Daily weather data for the years 1971 through 2004 were collected "on site" at the Aroostook Research Farm, as described by Baron et al. (1980). Mean, minimum, and maximum daily data were used to calculate respective monthly and seasonal weather summaries (winter, December–February; summer, June–August; spring, March–May; and summer, June–August). The summaries then were used as aggregated predictor variables to determine the direct and indirect effects of temperature and precipitation on fluctuations in aphid populations. Monthly summaries, as well as the summaries for spring and fall air temperatures were initially included in model construction, but they were not significant predictors of aphid population growth rates.

Data Analysis. Structural Equation Modeling (SEM; Pugesek et al. 2003, Grace 2006) was originally considered as a methodology to explore the relationships between natural enemies and weather on the population growth of aphids, but sample size (only 34 yr) prevented adequate estimation of model coefficients using the software AMOS (Arbuckle 2006). Therefore, we instead used Path Analysis, which is a similar approach to model building and is actually a predecessor of SEM (Wright 1934, Mitchell 2001). However, instead of modeling for predictive purposes as proposed by (Mitchell 2001), we used path analysis more as an exploratory tool for the purpose of developing conceptual models (Shipley 1997) that serve as a set of linked hypotheses. Because our main objective was to develop a conceptual model of potato infesting aphid population dynamics as a set of hypotheses, accepting a false null hypothesis was a big concern in this study. Therefore, in addition to using the traditional $P < 0.05$ cut-off level, we also gave consideration to $P < 0.10$ as a liberal guideline for determining potential factors that might affect aphid density flux. We feel that it is important to include effects that have potential to regulate potato-colonizing aphid species. At the same time, we suggest that these conclusions are only hypotheses and we do not have a strong degree of confidence in factors that are significant at levels $0.05 \leq P \leq 0.10$.

Fig. 1A illustrates the initial hypothesis and thus structure of the path model for each of the three potato infesting species and the total aphid population (densities of three species summed). Total aphid community was included in the analyses on the assumption that natural enemies might treat all three aphid species as a single food source. Our hypothesis was that weather factors had both direct effects on aphid intrinsic rate of growth ($\log(N_{(t+1)}/N_{(t)})$) and indirect

effects through the effects of natural enemies. Figure 1A does not include any correlations between weather factors because we found no evidence to support this model structure (correlation analyses, $P > 0.10$).

The intrinsic rate of growth was chosen as the index of population regulation to minimize the confounding of causal versus correlative factors in the interpretation of modeling results. We speculated that although population density is likely to work both ways (natural enemies decrease aphids, aphids increase natural enemies), intrinsic rate would not affect natural enemies at time t . In addition, we hypothesized that natural enemies and aphid populations other than the aphid species being modeled had direct effects on aphid intrinsic rate of growth over the 34-yr period. It was assumed that relationships between natural enemies were correlative and not causal because of similar numerical, functional responses, or both to the same prey or host resources.

Similar to weather data, we used aggregate predictor variables for the biotic factors. Natural enemies were represented as total predators, total parasitoids, or total disease mummies as a means of reducing the excessive number of potential predictor variables (there are five taxonomic groups of predators and one of those, the ladybeetles, is comprised of five or more species, depending upon the year). This is akin to using latent variables in structural equation models (Grace 2006) and also reduces the amount of type I experiment-wise error inflation and data dredging (Mitchell 2001). Aphid and natural enemy densities were estimated as an annual mean by integrating the within growing season time series generated by the weekly sampling as described by Southwood (1978) and performed in our previous analysis of aphid population dynamics (Alyokhin et al. 2005). Logarithm transformations of aphid and natural enemy densities were used in all models to stabilize variances. The overall correlation structure between exogenous predictor variables and endogenous dependent variables (see Total Causal Effect, Table 2) is arrived at by summing 1) the path coefficients for direct and then summing 2) the products of path coefficients and correlations for indirect paths from a given predictor of the dependent variable (Mitchell 2001). The strength of the effect assigned to unanalyzed causes ("U" on Fig. 1B–E) was calculated as $U = \sqrt{[1-r^2]}$ (Mitchell 2001). All coefficients were estimated by using general linear models and linear correlation analysis (SPSS 2006).

We first assessed the correlation structure of the data to determine the degree of serial autocorrelation (Wei 1990, SPSS 2006) that was expected to be a property of the long-term aphid dataset. We conducted ordinary least squares linear regression of years on the aphid intrinsic rate of growth and natural enemy populations over time. From this regression, the Durbin–Watson first order autocorrelation statistic was calculated using the residuals, and in conjunction with visual analysis of the residuals, evidence for first-order autocorrelations were evaluated (Chatterjee and Price 1991). Modeling several predictor variables apparently reduced the effect of serial autocor-

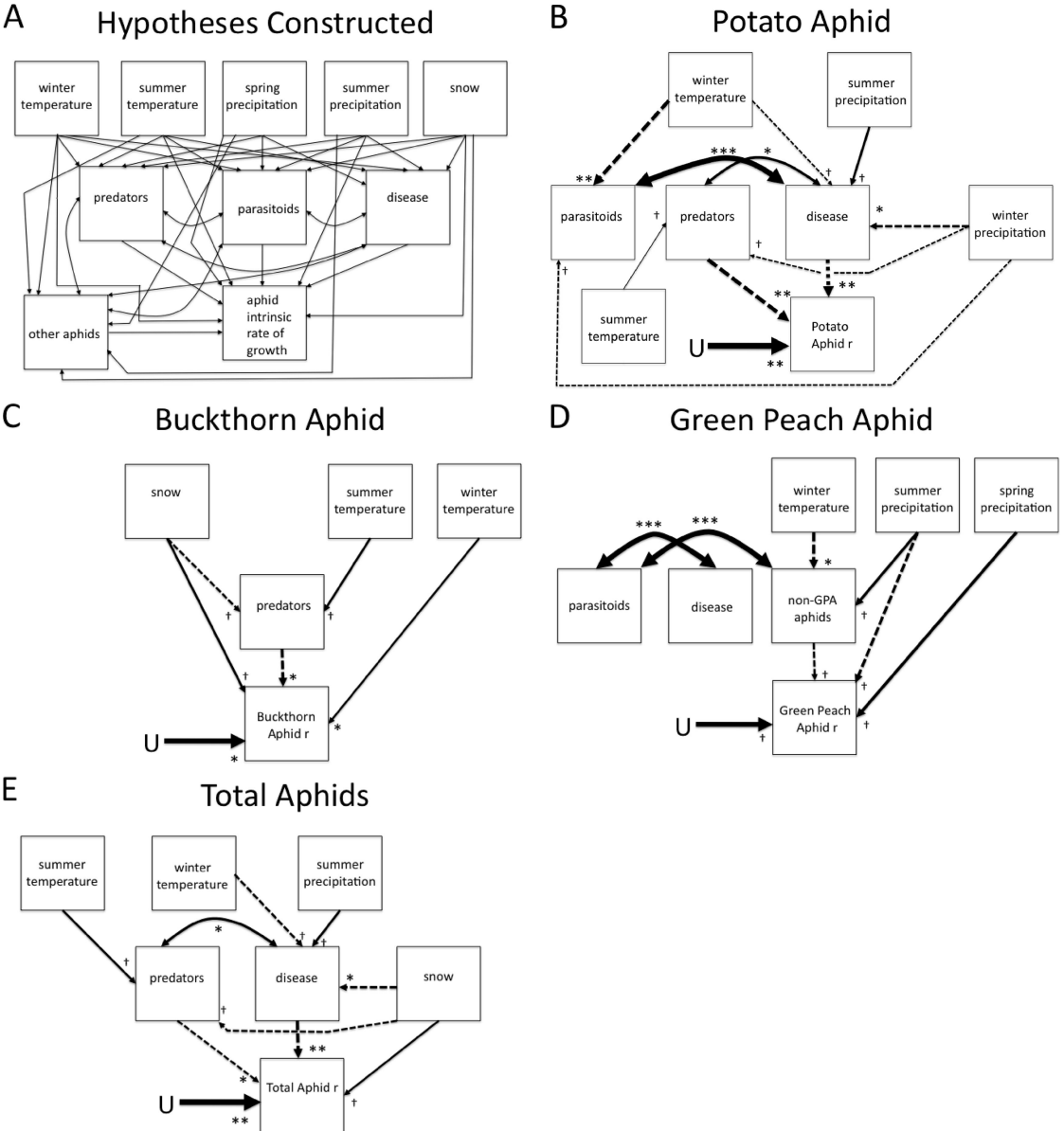


Fig. 1. Hypotheses for Path Analysis (A) and Path Analysis diagrams for three potato infesting species and the total aphids intrinsic rates of growth observed on potato plants between 1971 and 2004 in Presque Isle, ME, USA (B-E). Only significant relationships are shown (†, *, and ** are α levels of 0.10, 0.05, and 0.01). Straight lines are Path coefficients, curves are correlation coefficients, thickness of line denotes strength of relationship and solid line is a positive relationship and dashed line is a negative relationship. Unknown causes for the residual amount of variation unexplained by endogenous and exogenous factors affecting aphid intrinsic rate of growth is denoted by “U”.

relation as suggested by Chatterjee and Price (1991) and so transformations to adjust residuals were not necessary. The regression software in SPSS (SPSS 2006) was used to estimate path coefficients through estimation of partial regression coefficients (beta weights) (Pedhazier 1982). Direct and indirect effects on aphid intrinsic rate of growth were calculated using the path tracing decomposition method outlined by Knoke and Bohrnstedt (1994).

Path analysis was followed by linear regression (SPSS 2006) to assess the contributions of individual predator species or higher level predator taxa groupings to aphid population dynamics (change in aphid intrinsic rates of growth over time). To estimate which lower-level (species, genera, family, or order) natural enemy taxa might be responsible for regulating dynamics of aphid populations, we conducted further posthoc analyses. We used linear regression to esti-

Table 1. Path (standardized beta regression coefficients) and correlation coefficients that define relationships between exogenous and endogenous factors which explain variation in aphid intrinsic rates of growth

Variables ^a	Path coefficients or direct effects (probability >0) ^b							
	Parasitoids	Disease	Predators	Buckthorn aphid	Green peach aphid	Potato aphid	Total aphids	Aphids other than green peach aphids
Spring precipitation	0.010 (0.957)	0.129 (0.463)	0.248 (0.214)	−0.213 (0.274)	0.382 (0.061)	0.119 (0.447)	0.102 (0.538)	0.065 (0.730)
Summer precipitation	0.073 (0.698)	0.321 (0.073)	−0.267 (0.181)	−0.118 (0.604)	−0.394 (0.058)	−0.201 (0.278)	−0.189 (0.333)	0.349 (0.070)
Winter precipitation	−0.295 (0.075)	−0.341 (0.038)	−0.279 (0.088)	0.321 (0.069)	0.187 (0.300)	0.107 (0.453)	0.272 (0.078)	−0.210 (0.197)
Summer temp	0.088 (0.581)	0.201 (0.179)	0.299 (0.080)	−0.062 (0.711)	−0.066 (0.697)	−0.151 (0.272)	−0.130 (0.578)	0.058 (0.713)
Winter temp	−0.469 (0.008)	−0.291 (0.061)	−0.117 (0.499)	0.379 (0.049)	0.107 (0.569)	−0.100 (0.519)	0.076 (0.635)	−0.403 (0.019)
Parasitoids	–	0.766 (0.0001) ^c	0.117 (0.492) ^d	0.256 (0.412)	0.134 (0.671)	0.077 (0.767)	0.210 (0.427)	0.707 (0.0001)
Disease	0.766 (0.0001) ^c	–	0.333 (0.044) ^d	0.181 (0.622)	0.193 (0.603)	−0.473 (0.018)	−0.570 (0.011)	0.695 (0.0001) ^d
Predators	0.117 (0.492) ^c	0.333 (0.044) ^d	–	−0.379 (0.050)	−0.022 (0.912)	−0.480 (0.013)	−0.400 (0.025)	−0.138 (0.415) ^d
Other aphids ^e	–	–	–	−0.193 (0.446)	−0.285 (0.048)	−0.014 (0.952)	–	–
Variation in dependent variable explained	r ² = 0.280	r ² = 0.386	r ² = 0.217	r ² = 0.420	r ² = 0.396	r ² = 0.607	r ² = 0.542	r ² = 0.291
	P = 0.053	P = 0.009	P = 0.114	P = 0.041	P = 0.098	P = 0.001	P = 0.003	P = 0.056

^a Causal Predictor variables used to develop Path Coefficients.
^b Bold coefficients are those that are significant at $\alpha = 0.10$.
^c Correlation coefficients between natural enemies.
^d Correlation coefficients between natural enemies and density of aphids other than the green peach aphid.
^e Other aphids are the total densities of aphid species that are not the species under investigation, i.e. in modeling buckthorn aphid, the “other aphids” are the summed densities of green peach and potato aphid, the aphid species that are not buckthorn aphids.

mate the percent of variation explained in total predator density by densities of individual lower-level taxa. In addition, we used linear correlation to assess whether any of the significant lower-level taxa were colinear.

Results

Aphid Population Dynamics. Fig. 1 depicts the conceptual population dynamics models (path diagrams) for potato aphid (Fig. 1B), buckthorn aphid (Fig. 1C), green peach aphid (Fig. 1D), and total aphids (Fig. 1E). The models only include the significant (both $P < 0.05$ we are confident in, as well as $0.05 \leq P \leq 0.10$ we include as hypotheses) path coefficients, although all of the coefficients were estimated for each of the models (Table 1). It is apparent from inspection of the models that although all three species of aphids seem to be ecologically similar, the factors that govern their population growth are different.

Our interpretation of the potato aphid path model (Fig. 1B) is that populations are regulated by predators and diseases. There appears to be no direct weather effects on potato aphid intrinsic rate of growth (over the 34-yr period). However, the indirect effects of summer rain (positive relationship), winter temperature (negative relationship), and winter precipitation (negative relationship) are manifest through disease incidence. Summer temperature also indirectly affects potato aphid population growth through a positive causal relationship on predators. Of the three discussed effects, only winter precipitation is significant at $P \leq 0.05$, although all other effects are significant only at $P \leq 0.10$ and should be treated with caution (Table 1). Predators and diseases are correlated. This data leads to difficulty in separating the effects of each natural enemy group and also results in paths of indirect effects. Path coefficients (Table 1) suggest that disease and predator effects are similar in magnitude (−0.473 versus −0.480, respectively). Aphid parasitoids are affected by winter temperature and pre-

cipitation, but do not appear to affect aphid population growth.

Population dynamics of the buckthorn aphid appears to be different (Fig. 1C). Predators are the only natural enemy group involved in its regulation. There are several direct weather effects. Winter temperature, a positive effect ($P < 0.05$) and snow, a positive effect ($P < 0.10$) directly influence buckthorn aphid population dynamics with an effect-strength similar to

Table 2. Direct and indirect causal effects of predictors on aphid intrinsic rates of growth

	Direct causal effect	Indirect causal effect	Total causal effect	Unanalyzed causes (U)
Buckthorn aphid				0.777
Summer temp	+0.321	+0.106	+0.427	
Winter temp	–	−0.113	−0.113	
Winter precipitation	+0.379	–	+0.379	
Predators	−0.379	–	−0.379	
Green peach aphid				0.627
Winter temp	–	+0.115	+0.115	
Spring precipitation	+0.382	–	+0.382	
Summer precipitation	−0.394	+0.112	−0.282	
Non-green peach	−0.285	–	−0.285	
Aphids				
Potato Aphid				0.677
Summer temp	–	−0.188 ^a	−0.188	
Winter temp	–	+0.359 ^{ab}	+0.359	
Summer precipitation	–	−0.203 ^a	−0.203	
Winter precipitation	–	+0.158 ^a	+0.158	
Predators	−0.480	–	−0.480	
Disease	−0.473	–	−0.473	
Total aphids				0.842
Summer temp	–	−0.209 ^a	−0.209	
Winter temp	–	+0.205 ^a	+0.205	
Summer precipitation	–	−0.226 ^a	−0.226	
Winter precipitation	+0.272	+0.259 ^a	+0.531	
Predators	−0.570	–	−0.570	
Disease	−0.400	–	−0.570	

^a Includes unanalyzed effects due to correlative mediated effects of natural enemies.
^b Includes spurious correlation effect due to a common causal effect.

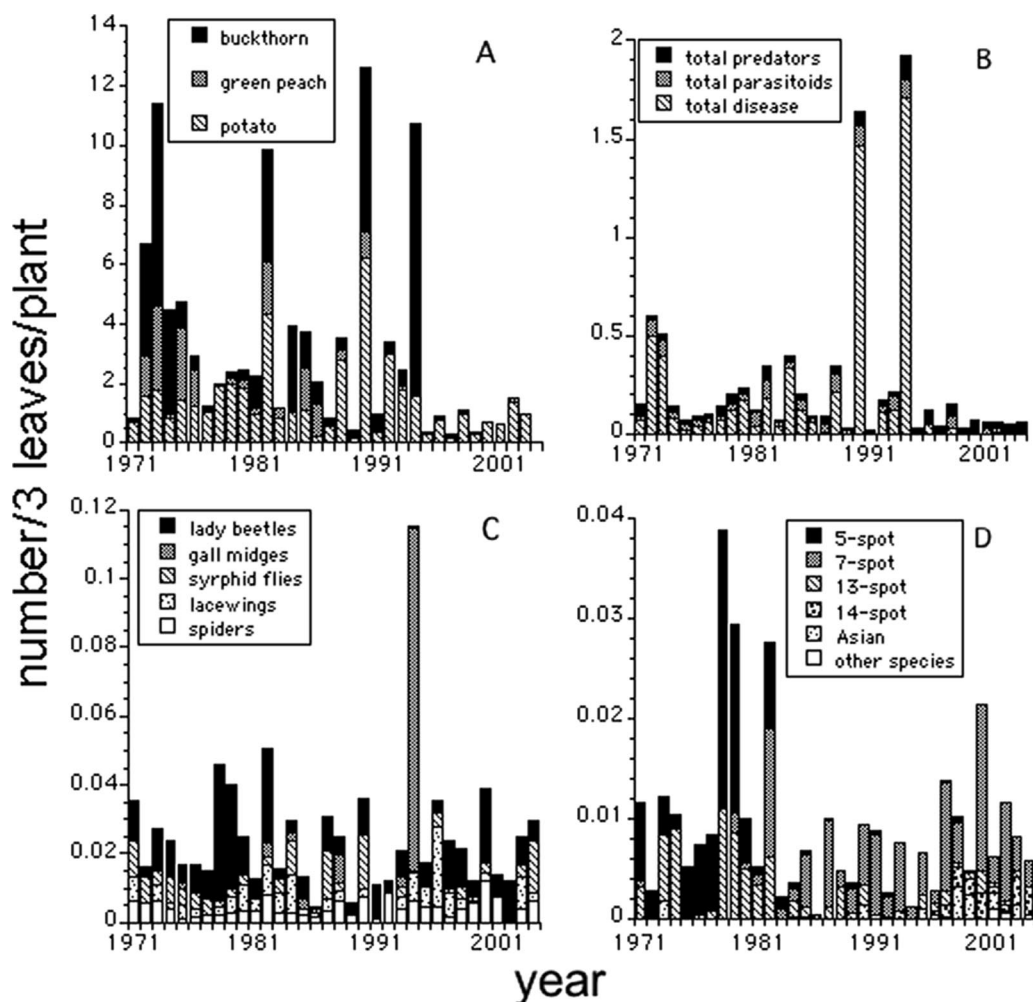


Fig. 2. Density time course (1971–2004) of potato aphid pest species (A), natural enemies segregated as predators, parasitoids and diseased cadavers (B), predators segregated as ladybeetles, predaceous and parasitic gall midges, syrphid flies, lacewings, and spiders (C), and lady beetles segregated into five species and a grouping of miscellaneous species (D).

predators (≈ 0.32 – 0.38) (Table 1). The negative impact of predators on aphid population growth rate ($P < 0.05$) is indirectly affected by the negative effect of snow ($P < 0.10$) and the positive effect of summer temperature ($P < 0.10$) on predators. Again, those factors where $P < 0.10$ we treat as hypotheses only.

Green peach aphid population dynamics (Fig. 1D) turn out to be the most different of the three aphid species. We did not detect direct involvement of natural enemies in the long-term population regulation of this species (Table 1). At the same time, combined population densities of the other two aphid species (potato aphids and buckthorn aphids) have a significant negative effect on the growth of the green peach aphid populations (Table 1). These combined aphid densities are negatively affected by parasitoids, disease, and winter temperatures. The only potentially significant direct weather effects ($P < 0.10$) on green peach aphids are those of summer rain (a negative effect) and spring rain (a positive effect) (Table 1).

Dynamics of the total aphid community (populations of all three species combined) (Fig. 1E) are most similar to the potato aphid dynamics. This similarity is most likely because of potato aphid being the dominant aphid species over the last 8 yr of the study (Fig. 2A). Predators and disease appear to be the most influential factors affecting community dynamics, with disease being a slightly stronger a force of mortality than predation (-0.570 , $P = 0.011$ versus -0.400 , $P = 0.025$; respectively). Winter precipitation in the form of snow is the only direct weather effect on aphid community rate of increase, and only at $P < 0.10$ (Table 1). However, many weather factors (summer rain, summer precipitation, winter precipitation, and winter temperature) may have an indirect effect on community rate of increase through natural enemies, although mostly at $P < 0.10$ (Fig. 1E, Table 1).

In all four conceptual population dynamics models, the magnitude of the regulatory effect pertaining to unanalyzed causes is substantial ("U" in Fig. 1B–E and

Table 2). The situation is similar with densities of the natural enemy populations, although we did not include that information in Fig. 1B–E to prevent clutter.

The total effects for each aphid model are shown in Table 2. The total causal effects on buckthorn aphid intrinsic rate of growth appear to be influenced mostly by temperature and winter precipitation, and also by predation. Summer temperature is most influential, winter precipitation and predation are equivalent, and winter temperature is the least influential. Natural enemies have no causal effects on green peach aphid intrinsic rate of growth. Spring precipitation is the most influential, followed by comparable influences of summer precipitation and sympatric nongreen peach aphid species abundances. Similar to buckthorn aphid, winter temperature is the least influential effect on green peach aphid intrinsic rate of growth. Potato aphid rate of growth is most influenced by predators and disease, although winter temperature is the most influential of the four significant weather factors. Fluctuations in the total aphid community appear to be influenced most heavily by predators, disease, and winter precipitation. Summer and winter temperatures and summer precipitation have half the influence of the other factors.

Natural Enemy Decomposition. Fig. 2B illustrates the composition of total disease, total parasitoids, and total predators on an annual basis over the 34-yr period. It is not surprising that disease is an important factor in determining fluctuations in growth rate of potato aphids and the total aphid community. During the first 24 yr of the study, disease(s) tended to be in very high incidence relative to the other natural enemy guilds in about half of the years. During the last 10 yr, when aphid abundance was generally low, diseases had become much less prominent. Parasitoids and predators (Fig. 2B) fluctuated in relative abundance, but in general over the 34-yr period the groups appeared to be subequal in incidence. Diseases and parasitoids were not identified to species, so we cannot be any more specific about these groups.

Predators were shown to be significant factors contributing to the regulation of buckthorn aphids, potato aphids, and the total aphid community. Most predators found associated with aphids on potato during this study are considered polyphagous, a few oligophagous. The list of recorded taxa included lady beetles (Coleoptera: Coccinellidae); predaceous midges (Coleoptera: Cecidomyiidae); green lacewings (Neuroptera: Chrysopidae); hover fly larvae (Diptera: Syrphidae); and a diverse group, spiders (Arachnida: Araneae). Upon inspection it would be very difficult to attribute which taxon was primarily responsible for predation on aphids. Figure 2C shows that the predator complex varied from year to year and it is reasonable to suggest that most if not all groups contributed to overall aphid predation. Lady beetles were the most abundant guild and constituted 38.3% of the total predator community (not including host-feeding hymenopterous parasitoids), followed by spiders (17.1%), hover fly larvae (15.6%), lacewing larvae (15.4%), and predatory midge larvae (13.6%). Decomposition of

the variance of total predator density over the 34 yr using a general linear analysis of variance (ANOVA) model suggests that the recorded predator community was fairly stable over time. However, only spiders and lacewings significantly explained any of the observed total variance in predators (19.1%, $P = 0.009$ and 21.6%, $P = 0.005$; respectively).

The lady beetle species composition in potato in Maine has been in flux over the 34-yr period of this study (Alyokhin and Sewell 2004) as new exotic species became established and native species were suppressed (Fig. 2D). Over this time the most abundant lady beetle was the exotic 7-spotted lady beetle, *Coccinella septempunctata* (L.), comprising 13.5% of total predator abundance and found during 27 of the 34 yr. It was followed by the transverse lady beetle *Coccinella transversoguttata* (F.) (11.6% of the total predator abundance and observed during 22 of the 34 yr), the 13-spotted lady beetle, *Hippodamia tredecimpunctata* L. (8.4% and 30 of 34 yr), the 14-spotted lady beetle, *Propylea quatuordecimpunctata* (L.) (1.8% and 10 of 34 yr), and the multicolored Asian lady beetle, *Harmonia axyridis* Pallas (1.6% and 12 of 34 yrs). Regressing each of the lady beetle abundances (logarithm transformed) on aphid intrinsic rate of growth for the years beginning when the species was first detected until the year it was last observed suggested that only *P. quatuordecimpunctata* appeared to contribute to regulating the buckthorn aphid ($\beta = -1.592$, $r^2 = 0.429$, $P = 0.043$). However, for this same time period *P. quatuordecimpunctata* abundance was highly correlated with that of *C. septempunctata* ($r = 0.725$, $P = 0.017$). Therefore, the conclusions regarding the role played by *P. quatuordecimpunctata* in controlling aphid populations are not obvious.

Discussion

Abiotic and biotic factors included in our model explained between 39.6 and 60.7% of the observed variation in the intrinsic rate of increase for the three tested aphid populations. Unanalyzed causes also made a substantial contribution, suggesting that a significant number of factors that drive the intrinsic rate of growth have not been considered in the model, or that there was insufficient power to detect other sources that explain variation. One possible factor not included in the analyses is migration. It is known to affect the dynamics of aphid populations (Dixon 1985, Ward et al. 1998), including potato-colonizing species (Shands and Simpson 1959, Hodgson 1991, Lamb et al. 1997), but was not measured when the data used in this study were collected. Other factors outside of the scope of the current study were intraspecific interactions, genotype and condition of the host plants, an interactions of those factors, or all three. For example, Brunissen et al. (2009) reported that conspecific preinfestation of potato plants by potato aphids led to a considerable reduction in duration of phloem sap ingestion, probably because of the induction of a phloem-located antixenosis. Conversely, previous infestation by the green peach aphid on three different peach

cultivars resulted in an improvement of conspecific performance (Sauge et al. 2002, 2006). Yet another possible factor could have been intraguild predation among natural enemies, which is common for the taxonomic groups included in this study (Snyder and Ives 2001, Finke and Denno 2004).

Weather factors considered in our analyses contributed to the regulation of aphid populations, either directly or through natural enemies. However, in most cases direct weather effects were detectable only at $P < 0.10$, so that they remain as a relatively weak hypotheses for our conceptual model. Our earlier study (Alyokhin et al. 2005) found strong evidence of density-dependent regulation, but relatively minor effects of density-independent weather factors. Similarly, density-independent weather effects were negligibly small or nonexistent in regulating populations of the Turkey-oak aphid *Myzocallis boerneri* Stroyan (Jarošík and Dixon 1999), galling aphid *Baizongia pistaciae* (L.) (Wool 2002), and the bird-cherry aphid *Rhopalosiphum padi* L. (Bommarco et al. 2007). To the contrary, both density-independent and density-dependent factors were found to be important by Maudsley et al. (1996) for the grain aphid *Sitobion avenae* F. and the bird-cherry aphid *R. padi* and by Slosser et al. (1998) for the cotton aphid *Aphis gossypii* Glover. Although we believe that the potential role of abiotic factors in regulating aphid populations in our study should not be ignored, there is definitely a degree of uncertainty surrounding their direct importance. To acknowledge this, we state in the discussion below that factors significant at $P < 0.10$ may have had an effect on aphid populations, but factors significant at $P < 0.05$ had such an effect.

Spring precipitation may have had a direct positive effect on the growth of the green peach aphid population, possibly through its effect on the quality of host plants (A'Brook 1981, Maudsley et al. 1996). It did not affect any other insects. Summer precipitation may have had a direct negative effect on the green peach aphid. It also may have promoted the growth of entomopathogenic fungi, thus indirectly suppressing populations of potato aphids that were strongly affected by fungal disease. Winter precipitation may have had a positive effect on buckthorn aphids, which might have been plant-mediated in origin as speculated above for the effect of spring precipitation on the green peach aphids. At the same time, winter precipitation may have had a negative effect on parasitoids and predators, and had a negative effect on entomopathogenic fungi. Although thick snow cover may increase survivorship of overwintering insects by preventing soil from freezing, it also results in more water-saturated soils in the spring. This saturation might increase mortality of overwintering natural enemies, particularly the lady beetles, through drowning and promoting epizootics of fungal disease (Jean et al. 1990, Harwood et al. 2006, Riddick 2006, Labrie et al. 2008). Spring flooding would not have had such an effect on aphids because they overwinter above the ground on trees.

Higher summer temperatures may have resulted in higher incidence of predators, but did not affect other insects or disease. All predators recorded in the current study are rather mobile, at least as adults. Movement, especially by flight, is very energy-demanding, and could be significantly enhanced by high temperature and solar irradiation (Dudley 2000, Goldsworthy and Joyce 2001). Therefore, it is conceivable that their habitat-colonizing ability was enhanced by higher summer temperatures. Winged aphids and their parasitoids are small in size, weak fliers, and largely rely on air currents for dispersal. Fungal spores are also passively dispersed by the wind. Therefore, they were less likely to be affected by temperature. Higher winter temperatures resulted in higher population growth of buckthorn aphids, most likely because of the lower winter mortalities. Unexpectedly, they also led to lower populations of parasitoids and, possibly, entomopathogenic fungi. This decrease might have been because of the higher overwintering survivorship of their natural enemies, but we do not yet have sufficient data for making definite conclusions.

Natural enemies significantly ($P < 0.05$) influenced the population growth of two aphid species. Potato aphids were negatively affected by both fungal disease and predators, although buckthorn aphids were negatively affected by predators only. Annual field studies conducted from 1952 to 1959 (Shands et al. 1963, 1972a) also found that potato aphid was the most affected by fungi among the aphid species in Maine potatoes, although the authors thought that the fungal epizootics suppressed populations of all potato-colonizing species. Significant predator role in regulating aphid populations is widely known (Dixon 2000) and has been previously demonstrated for potato-colonizing aphids in Maine (Shands et al. 1972b).

Parasitoids did not have a noticeable effect on the population growth of any of the three aphid species. Although certainly different from many other systems, this finding is consistent with the earlier report by Shands et al. (1963, 1972c). Also, Gross et al. (2005) found that increases in parasitism of the pea aphid *Acyrtosiphon pisum* (Harris) by the specialist parasitoid *Aphidius ervi* (Haliday) (Hymenoptera: Aphididae) did not coincide with declines in aphid population growth rates, and parasitism could not have been responsible for the density-dependent regulation of aphid populations observed in the field.

Despite large variation among the years of the study, there was no obvious shift in total natural enemy abundance or in the ratio of different taxonomic groups. However, only lady beetles were identified to a species, with a dramatic change in community composition detected over the years. It is possible that a similar shift would have been noticed for other taxonomic groups should they been studied in more detail. Replacement of native lady beetles by introduced species is a widely occurring phenomenon (Snyder and Evans 2006), and northern Maine is no exception (Alyokhin and Sewell 2004, Finlayson et al. 2008). Interestingly, we detected evidence that population growth of the buckthorn aphid is affected by the

exotic lady beetle *P. quatuordecimpunctata*. Although *P. quatuordecimpunctata* abundance was highly correlated with that of *C. septempunctata*, the latter is also a non-native species. Therefore, we believe that the present results support our earlier hypothesis (Alyokhin et al. 2005) that establishment of non-native lady beetles is responsible for the decline of the buckthorn aphid in Maine potatoes.

We did not detect any natural enemy effect on the growth of green peach aphid populations. Although this might have been true at the location and over the time period of our study, in general biological control can be a valuable option for managing this species (Snyder et al. 2006). At the same time, we detected a significant negative influence of interspecific interactions with the other two aphid species. This is in agreement with Alyokhin et al. (2005), who detected evidence for density dependence in green peach aphid over a 55-yr period. Neither potato aphids nor buckthorn aphids were affected by heterospecifics. Denno et al. (1995) reviewed 193 pair-wise interactions among insect herbivores and found evidence of competition for the 93% of species with piercing-sucking mouthparts, with most interactions being asymmetric. Furthermore, Dugravot et al. (2007) reported that green peach aphids less readily accepted noninfested leaves on potato plants that had other leaves infested by potato aphids, possibly because of induced plant defense. Conversely, in the study by Brunissen et al. (2009), feeding behavior of potato aphids was not affected on plants previously infested by green peach aphids, but potato aphids were more attracted to and had a faster population build-up on those plants. Together with our results, this information appears to suggest that green peach aphid is a weaker competitor on potato plants compared with the other two species.

Differential population regulation mechanisms detected in the current study might at least partially explain coexistence of three ecologically similar aphid species sharing the same host plant. When species respond differently to a varying environment, as is the case in the current study, it is possible for the otherwise inferior competitor to persist (Chesson and Huntly 1989). Therefore, the observed difference in regulatory mechanisms was likely important for allowing the three populations to coexist over the 34-yr period of time.

From a management perspective, our results suggest that careful pesticide use to minimize negative impacts on predators and entomopathogenic fungi will contribute to reducing growth of potato aphid and buckthorn aphid populations, particularly in the years when weather conditions are not favorable for these two groups of natural enemies. Also, tolerating non-damaging densities of the potato aphid and buckthorn aphid might prevent build-up in the green peach aphid, which is more damaging because of higher competency in transmitting viral diseases of potato (Radcliffe et al. 1993). Future experimental confirmation of these hypotheses will significantly contribute to improving ecologically-based pest management in potato crops.

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References Cited

- A'Brook, J. 1981. Some observations in west Wales on the relationship between numbers of alate aphids and weather. *Ann. Appl. Biol.* 97: 11–15.
- Alyokhin, A., and G. Sewell. 2004. Changes in a lady beetle community following the establishment of three alien species. *Biol. Invasions* 6: 463–471.
- Alyokhin, A., F. A. Drummond, and G. Sewell. 2005. Density-dependent regulation in populations of potato-colonizing aphids. *Popul. Ecol.* 47: 257–266.
- Arbuckle, J. L. 2006. AMOS 7.0 User's Guide. Amos Development Corporation, Spring House, Pennsylvania.
- Baron, W. R., D. C. Smith, H. W. Borns, Jr., J. Fastook, and A. E. Bridges. 1980. Long-time series temperature and precipitation records for Maine, 1808–1978. *Life Sciences and Agriculture Experiment Station Bulletin 771*, University of Maine, Orono, Maine.
- Berryman, A. A. 1981. *Population systems*. Plenum, New York.
- Blackman, R. L., and V. F. Eastop. 2000. *Aphids on the world's crops: an identification and information guide*, 2nd ed. Wiley, Chichester, United Kingdom.
- Bommarco, R., S. Wetterlind, and R. Sigvald. 2007. Cereal aphid populations in non-crop habitats show strong density dependence. *J. Appl. Ecol.* 44: 1013–1022.
- Brunissen, L., A. Cherqui, Y. Pelletier, C. Vincent, and P. Giordanengo. 2009. Host-plant mediated interactions between two aphid species. *Entomol. Exp. Appl.* 132: 30–38.
- Chatterjee, S., and B. Price. 1991. *Regression analysis by example*. Wiley, New York.
- Chesson, P., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends Ecol. Evol.* 4: 293–298.
- Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annu. Rev. Entomol.* 40: 297–331.
- Dixon, A.F.G. 1985. *Aphid ecology*. Blackie, Glasgow, Scotland.
- Dixon, A.F.G. 2000. *Insect predator-prey dynamic: ladybird beetles and biological control*. Cambridge University Press, Cambridge, United Kingdom.
- Dudley, R. 2000. *The biomechanics of insect flight*. Princeton University Press, Princeton, New Jersey.
- Dugravot, S., L. Brunissen, E. Letocart, W. F. Tjallingii, C. Vincent, P. Giordanengo, and A. Cherqui. 2007. Local and systemic responses induced by aphids in *Solanum tuberosum* plants. *Entomol. Exp. Appl.* 123: 271–277.
- Emlen, J. M. 1984. *Population biology*. Macmillan, New York.
- Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. *Nature* 429: 407–410.
- Finlayson, C. J., K. M. Landry, and A. V. Alyokhin. 2008. Abundance of native and non-native lady beetles (Coleoptera: Coccinellidae) in different habitats in Maine. *Ann. Entomol. Soc. Am.* 101: 1078–1087.
- Goldsworthy, G., and M. Joyce. 2001. Physiology and endocrine control of flight, pp. 65–86. *In* I. P. Woiwod, D. R. Reynolds, and C. D. Thomas (eds.), *Insect movement*.

- mechanisms and consequences. CABI Publishing, Wallingford, United Kingdom.
- Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, United Kingdom.
- Gross, K., A. R. Ives, and E. V. Nordheim. 2005. Estimating fluctuating vital rates from time-series data: a case study of aphid biocontrol. *Ecology* 86: 740–752.
- Hajek, A. 2004. Natural enemies: an introduction to biological control. Cambridge University Press, Cambridge, United Kingdom. 1–378.
- Hanski, I. 1990. Density dependence, regulation and variability in animal populations. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 330: 141–150.
- Hanski, I., I. Woiwod, and J. Perry. 1993. Density dependence, population persistence, and largely futile arguments. *Oecologia* 95: 595–598.
- Harwood, J. D., C. Ricci, R. Romani, K. M. Pitz, A. Weir, and J. Obyrcki. 2006. Prevalence and association of the laboulbenian fungus *Hesperomyces virescens* (Laboulbeniales: Laboulbeniaceae) on coccinellid hosts (Coleoptera: Coccinellidae) in Kentucky. *Eur. J. Entomol.* 103: 799–804.
- Hirose, Y. 2006. Biological control of aphids and coccids: a comparative analysis. *Popul. Ecol.* 48: 307–315.
- Hodgson, C. 1991. Dispersal of apterous aphids (Homoptera: Aphididae) from their host plant and its significance. *Bull. Entomol. Res.* 81: 417–427.
- Holyoak, M., and J. H. Lawton. 1992. Detection of density dependence from annual censuses of bracken-feeding insects. *Oecologia* 91: 425–430.
- Holyoak, M., and J. H. Lawton. 1993. Comments arising from a paper by Wolda and Dennis: using and interpreting the results of tests for density dependence. *Oecologia* 95: 592–594.
- Jarošík, V., and A.F.G. Dixon. 1999. Population dynamics of a tree-dwelling aphid: regulation and density-independent processes. *J. Anim. Ecol.* 68: 726–732.
- Jean, C., D. Coderre, and J. C. Tourneur. 1990. Effects of temperature and substrate on survival and lipid consumption of hibernating *Coleomegilla maculata* Lengi (Coleoptera: Chrysomelidae). *Environ. Entomol.* 19: 1657–1662.
- Knoke, D., and G. W. Bohrnstedt. 1994. Statistics for social data analysis, 3rd ed. Peacock, Ithasca, Illinois.
- Labrie, G., D. Coderre, and E. Lucas. 2008. Overwintering strategy of multicolored Asian lady beetle (Coleoptera: Coccinellidae): cold-free space as a factor of invasive success. *Ann. Entomol. Soc. Am.* 101: 860–866.
- Lamb, R. J., I. L. Wise, and P. A. MacKay. 1997. Photoperiodism and seasonal abundance of an aphid, *Macrosiphum euphorbiae* (Thomas), in oilseed flax. *Can. Entomol.* 129: 1049–1058.
- Lewellen, R. H., and S. H. Vessey. 1998. Modeling biotic and abiotic influences on population size in small mammals. *Oecologia* 113: 210–218.
- Maudsley, M. J., A. MacKenzie, J. I. Thacker, and A.F.G. Dixon. 1996. Density dependence in cereal aphid populations. *Ann. Appl. Biol.* 128: 453–463.
- Mitchell, R. J. 2001. Path analysis, pollination, pp. 217–234. In S. M. Scheiner and J. Gurevitch (eds.), *Design and analysis of ecological experiments*. Oxford University Press, Oxford, United Kingdom.
- Nowicki, P., S. Bonelli, F. Barbero, and E. Balletto. 2009. Relative importance of density-dependent regulation and environmental stochasticity for butterfly population dynamics. *Oecologia* 161: 227–239.
- Pedhazur, E. J. 1982. Multiple regression in behavioral research, 2nd ed. Holt, Reinhart, and Winston, New York.
- Pianka, E. R. 1974. *Evolutionary ecology*. Harper and Row, New York.
- Pugesek, B. H., A. Tomer, and A. von Eye. 2003. *Structural equation modeling, applications in ecological and evolutionary biology*. Cambridge University Press, Cambridge, United Kingdom.
- Radcliffe, E. B., K. L. Flanders, and D. W. Ragsdale. 1993. Management of aphids and leafhoppers, pp. 103–115. In R. C. Rowe, (ed.), *Potato health management*. APS Press, St. Paul, Minnesota.
- Riddick, E. W. 2006. Influence of host gender on infection rate, density and distribution of the parasitic fungus, *Hesperomyces virescens*, on the multicoloured Asian lady beetle, *Harmonia axyridis*. *J. Insect Sci.* 6: (insectscience.org/6.42).
- Rothery, P., I. Newton, L. Dale, and T. Wesolowski. 1997. Testing for density dependence allowing for weather effects. *Oecologia* 112: 518–523.
- Royama, T. 1977. Population persistence and density dependence. *Ecol. Monogr.* 47: 1–35.
- Royama, T. 1992. *Analytical population dynamics*. Chapman & Hall, London, United Kingdom.
- Sauge, M. H., J. P. Lacroze, J. L. Poëssel, T. Pascal, and J. Kervella. 2002. Induced resistance by *Myzus persicae* in the peach cultivar 'Rubira'. *Entomol. Exp. Appl.* 102: 29–37.
- Sauge, M. H., F. Mus, J. P. Lacroze, T. Pascal, J. Kervella, and J. L. Poëssel. 2006. Genotypic variation in induced resistance and induced susceptibility in the peach *Myzus persicae* aphid system. *Oikos* 113: 305–313.
- Sequeira, R., and A.F.G. Dixon. 1997. Population dynamics of tree-dwelling aphids: the importance of seasonality and time scale. *Ecology* 78: 2603–2610.
- Shands, W. A., and G. W. Simpson. 1959. Characteristics of aphid-population growth on potatoes in northeastern Maine. *Ann. Entomol. Soc. Am.* 52: 117–121.
- Shands, W. A., G. W. Simpson, and L. B. Reed. 1954. Subunits for estimating aphid abundance on potatoes. *J. Econ. Entomol.* 47: 1024–1027.
- Shands, W. A., G. W. Simpson, and I. M. Hall. 1963. Importance of entomogenous fungi in controlling aphids on potatoes in northeastern Maine. The Maine Agricultural Experiment Station Technical Series Bulletin T6, University of Maine, Orono, Maine.
- Shands, W. A., G. W. Simpson, I. M. Hall, and C. C. Gordon. 1972a. Further evaluation of entomogenous fungi as a biological control agent of aphid control in northeastern Maine. Life Sciences and Agriculture Experiment Station Bulletin 58, University of Maine, Orono, Maine.
- Shands, W. A., G. W. Simpson, H. E. Wave, and C. C. Gordon. 1972b. Importance of arthropod predators in controlling aphids on potatoes in northeastern Maine. Life Sciences and Agriculture Experiment Station Technical Bulletin 54, University of Maine, Orono, Maine.
- Shands, W. A., G. W. Simpson, and C. C. Gordon. 1972c. Survey of internal parasites of potato-infesting aphids in northeastern Maine, 1963 through 1969. Life Sciences and Agriculture Experiment Station Technical Bulletin 60, University of Maine, Orono, Maine.
- Shipley, B. 1997. Exploratory path analysis with applications in ecology and evolution. *Am. Nat.* 149: 1113–1138.
- Sinclair, A.R.E., and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. *Oikos* 75: 164–173.
- Slosser, J. E., W. E. Pinchak, and D. R. Rummel. 1998. Biotic and abiotic regulation of *Aphis gossypii* Glover in west Texas dryland cotton. *Southwest. Entomol.* 23: 31–65.

- Snyder, W. E., and E. W. Evans. 2006. Ecological effects of invasive arthropod natural enemies. *Annu. Rev. Ecol. Syst.* 37: 95–112.
- Snyder, W. E., and A. R. Ives. 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* 82: 705–716.
- Snyder, W. E., G. B. Snyder, D. L. Finke, and C. S. Straub. 2006. Predator biodiversity strengthens herbivore suppression. *Ecol. Lett.* 9: 789–796.
- Southwood, T.R.E. 1978. Ecological methods, with particular reference to the study of insect populations, 2nd ed. Chapman & Hall, London, United Kingdom.
- SPSS. 2006. SPSS 15.0 Brief Guide. SPSS Inc., Chicago, Illinois.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis, pp. 17–40. *In* N. Cappuccino and P. Price (eds.), *Population dynamics: new approaches and synthesis*. Academic, San Diego.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* 73: 289–305.
- Ward, S. A., S. R. Leather, J. Pickup, and R. Harrington. 1998. Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts. *J. Anim. Ecol.* 67: 763–773.
- Wei, W.W.S. 1990. Time series analysis: univariate and multivariate methods. Addison-Wesley Publishing Company, New York.
- Wellings, P. W., R. J. Chambers, A.F.G. Dixon, and D. P. Aikman. 1985. Sycamore aphid numbers and population density. I. Some patterns. *J. Anim. Ecol.* 54: 411–424.
- Woiwod, I. P., and I. Hanski. 1992. Patterns of density dependence in moths and aphids. *J. Anim. Ecol.* 61: 619–629.
- Wolda, H., and B. Dennis. 1993. Density dependence tests, are they? *Oecologia* 95: 581–591.
- Wolda, H., B. Dennis, and M. L. Taper. 1994. Density dependence tests, and largely futile comments: answers to Holyoak and Lawton (1993) and Hanski, Woiwod and Perry (1993). *Oecologia* 98: 229–234.
- Wool, D. 2002. Herbivore abundance is independent of weather? A 20-year study of a galling aphid *Baizongia pistacia* (Homoptera: Aphidoidea). *Popul. Ecol.* 44: 281–291.
- Wright, S. 1934. The method of path coefficients. *Ann. Math. Stat.* 5: 161–215.

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