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RESEARCH ARTICLE

Long-term population dynamics of an insect in a simple food web under a changing environment

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Abstract

1. Weather conditions are important for the population dynamics of "cold-blooded" animals like insects, with both direct and indirect effects (via the food web). How weather, in combination with other factors, generates population change, and how such effects change over time, are important questions in times of climate change.
2. We monitored an insect seed predator population during a 36-year period of changing weather patterns. The insect is part of a simple food web dominated by seed consumption and lacking natural enemies. Environmental conditions were relatively stable during the first half of the study, but patterns changed during the latter half. Areas of host plant patches increased and seed production entered a strong bi-annual pattern.
3. Insect abundance was measured twice during the yearly life cycle, before and after summer reproduction, and seed resources and competitor densities were measured at the end of the summer.
4. We fit a population model to abundance data to investigate the population dynamics of the insect in relation to changing patterns in weather conditions and food resources.
5. There were both direct and indirect effects of weather, operating at multiple time scales. Abundant sunshine during summer resulted in increased population growth during the same period, but it also resulted in increased survival the following winter. Population growth further depends on seed set the previous summer, which in turn depends on summer rainfall and is likely affected by climate change. This implies indirect weather effects at both short-term and decadal time scales.
6. The new pattern of seed production seems to have led to increased average insect abundance but did not otherwise lead to clear changes in the dynamics of the population. This can be explained by weak regulation of the dynamics of the insect such that short-term environmental variation leads to long unstable population fluctuations.

7. Our study illustrates how insect responses to drastic changes in their environment can be subtle, slow, and hard to detect, manifested by long-term fluctuations. This highlights the importance of long-term data and mechanistic understandings of population dynamics to assess the consequences of changing weather and climate on insects.

KEYWORDS
climate change, landscape scale, long-wave fluctuations, Lygaeinae, population dynamics, time lags, weather mechanisms

1 | INTRODUCTION

Weather generally has strong effects on the dynamics of insect populations, and in times of climate change and general concern about the fate of insect populations, we need to better understand how changing weather patterns translate into insect population change (Abarca & Spahn, 2021; Boggs, 2016; Harvey et al., 2023; Moritz & Agudo, 2013; Müller et al., 2023; Wagner, 2020). Populations can be affected via multiple pathways, both directly on the focal species and indirectly via effects from interacting organisms. Direct effects may concern rates of development, survival, reproduction, and migration of insects (Bale et al., 2002). Effects may be complex, act via various life stages, and be manifested with various degrees of time lags (Azerefegne et al., 2001; Forister et al., 2011; Ogilvie & CaraDonna, 2022; Solbreck, 1995). This also pertains to the indirect weather effects via food resources, competitors, and enemy species (Barton & Ives, 2014; DeLucia et al., 2012; Frank, 2021; Hambäck, 2021; Johnson & Haynes, 2023; Pepi et al., 2018; Solbreck et al., 2022).

Long-term field data are of central importance to explore the mechanisms by which weather affects population dynamics in a changing world. However, the statistical analysis of such time series data should not stand alone. Weather variables are potentially innumerable, measurement errors may be large, and there is always a risk of obtaining spurious relationships. It is thus important to evaluate statistical findings against detailed biological knowledge of the target insect and its food web interactions (Benton et al., 2006; Boggs & Inouye, 2012; Knape & de Valpine, 2011; Matter et al., 2011).

What are the potential temporal changes in system dynamics to be found in long-term studies? Will populations respond in the same way in the future as before, or will dynamics depend on the specific period during which the system is studied? Will the frequency and impact of unusual extreme events change with time? Responses to changes are difficult to predict as they may depend on many case-specific factors (Vázquez et al., 2017). Some population systems may be pushed into new dynamic regimes in response to climate change (Pepi et al., 2021; Turner et al., 2020). Alternatively, systems may show various degrees of resilience to environmental change, making it difficult to discern effects of new environmental regimes. In the words of Ådahl et al. (2006) "climate change does not always translate into population change in an intuitive way".

Long-term studies of insect responses to weather are numerous, but there is a strong bias regarding taxa and methods employed. Studies of butterflies and pests abound, as do studies employing density indices rather than more detailed density measures. Rarely is more than one life history stage considered. We need data from a wider range of taxonomic groups and from species with different ecological roles (Boggs, 2016). There is also a need for more precise population estimates and measures from multiple life history stages to aid in unravelling mechanisms of weather effects and responses to a new climate (Ådahl et al., 2006; Azerefegne et al., 2001; Radchuk et al., 2013).

In this paper we are concerned with the long-term, landscape scale population dynamics of *Lygaeus equestris*, belonging to the Heteroptera, a group underrepresented in population studies (Musolin, 2007). The insect was studied for 36 years (1977–2012) in a coastal area in south-eastern Sweden. It is a non-pest seed predator, feeding on the perennial herb, White Swallowwort, *Vincetoxicum hirundinaria*. Previous studies of the insect and its host plant provide detailed information about biological and ecological interactions as well as habitat change (Solbreck, 1995, 2012; Solbreck & Ives, 2007; Solbreck & Knape, 2017). This allows us to link statistical patterns of population change to specific biological mechanisms.

The insect life cycle is relatively simple with the same feeding niche for nymphs and adults, and it is part of a simple trophic web with no enemies and only one presumptive competitor species in the region of study. The simple web allows us to keep track of all important web interactions. Finally, the study area underwent little land use change during the study period, isolating climate as the most likely long-term driver influencing the system.

During the first 18 years of the study no effects of climate change were evident (Solbreck, 1995). However, beginning in the early 1990's, host plant patches started to increase in areal cover to reach a three-fold increase at the end of the study period. This was evidently a response to increasing temperatures (Solbreck, 2012). The number of seeds produced by the host plant also increased, reaching an extreme in 2005 with four times more seeds than the previously observed maximum, which was followed by a series of years with alternating very low and very large seed production (Solbreck & Knape, 2017). The effects of these changing patterns in seed resources on the dynamics of the insect population have not been previously explored. We here use landscape level data of the pre- and post-summer population size of the bug population in combination with weather data and data on seed abundance to investigate how the dynamics of the population and its response to weather and climate have been affected by the changing patterns of resource fluctuations.

2 | MATERIALS AND METHODS

2.1 | Organisms and study area

Lygaeus equestris (L.) (Heteroptera, Lygaeidae) is the only Swedish representative of the subfamily Lygaeinae, a mainly tropical group with many aposematic species (Schuh & Slater, 1995). The insect usually has one generation a year (Figure 2), but in very warm summers, there may be a partial second generation (Solbreck, 1991; Solbreck & Sillén-Tullberg, 1981). It overwinters as an adult, often in large congregations in sun-exposed places such as south-facing rock walls with crevices (Figure 1d). On sunny days in spring, the insects fly from the overwintering sites to host plant patches where they feed and breed (Solbreck, 1976).

Feeding after over-wintering is essential for egg production in females (they are “income breeders”) (Solbreck, 1972). The eggs are laid in the ground in clutches of usually 28–56. Egg-laying is spread out over several weeks, and the total egg production may exceed 1000. Usually, nymphs can be seen from June and new adults from early July. They may feed on the seeds of several herb species, but they prefer those of White Swallowwort, *Vincetoxicum hirundinaria* Medicus (L.) (Apocynaceae), and they are more fecund on this species (Kugelberg, 1974). Furthermore, *L. equestris* is an aposematic insect, and the degree of aposematism is enhanced by feeding on this plant (Tullberg et al., 2000).

White Swallowwort is a long-lived perennial herb which grows on sun-exposed rocky areas (Figure 1a) and along forest margins. It forms dense tufts of from a few to over 100 shoots. The plants flower mainly in June and July, with fruit production dominating in July–August. Flower production is rather constant from year to year, whereas fruit production is extremely variable (Solbreck & Knape, 2017).

The plant has a distinctly patchy distribution on the landscape scale, each patch consisting of several individuals. (We define a patch as being separated from conspecific plants by at least 25 m.) In the main 3 km^2 study area at Tullgarn (58°57′ N, 17°36′ S), about 50 km SSW of Stockholm, there were 32 *V. hirundinaria* patches in 2012 ranging in size from 0.25 to about 700 m^2 (measured as ground area covered by the plant).

Lygaeus equestris is both a pre- and a post-dispersal seed predator. Both nymphs and adults feed on the ovulae in the flowers, on developing seeds in the fruit (sometimes called pods) and on dry seeds on the ground (Figure 1e). However, functionally, *L. equestris* is primarily a post-dispersal seed predator. The density of seeds on the ground from the previous year often limits *L. equestris* populations (Solbreck, 1995).

The insect prefers dry, sun-exposed habitats with patches of bare ground. It needs to bask in the sun to raise its body temperature (Solbreck, 1976) and prefers to lay eggs in the ground among loose litter. The combination of preferences for food plants, microclimatic conditions as well as for egg laying substrate makes *L. equestris* confined to the patches of *V. hirundinaria* during the summer.

The new generation adults feed intensely and accumulate a large fat body. When fully fed, usually in late August–September, they enter a flight period and move to the overwintering sites (Solbreck, 1972).

In addition to the autumn and spring flights to and from overwintering sites, there may also be flights during the summer in response to local food shortages. There is thus much movement between host plant patches. However, the study area (a peninsula) was chosen to minimize movements outside the area. Marking experiments also demonstrate that the bugs often move between host plant patches within this study area but much less so between the study area and outside areas (Solbreck & Sillén-Tullberg, 1990).

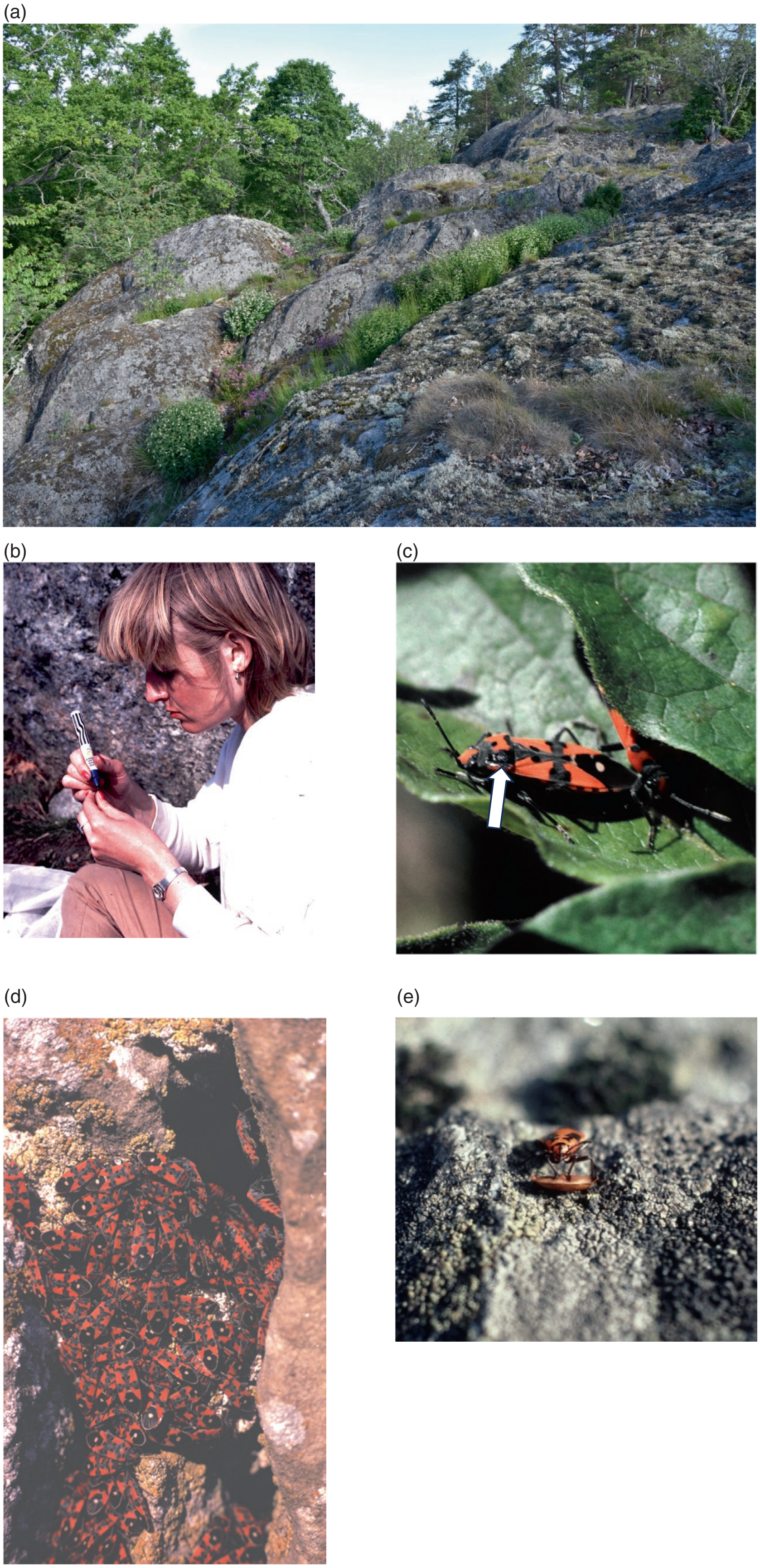
Three insect species, in addition to *L. equestris*, feed on *V. hirundinaria* in the study area. There is one leaf feeder *Abrostola asclepiadis* (Denis and Schiffermüller) (Lepidoptera, Noctuidae) and a flower gall midge *Contarinia vincetoxici* Kieffer (Diptera, Cecidomyiidae) (Solbreck et al., 2022; Solbreck & Widenfalk, 2020). Both species are rare in relation to their food resources, and their effects on seed production are negligible in the study area. The third species, *Euphranta connexa* (Fabr.) (Diptera, Tephritidae), is a monophagous predispersal seed predator. The larva feeds on the seeds in the developing fruit of the host plant. *Euphranta connexa* is an important seed predator on *V. hirundinaria*. Its population dynamics are largely determined by the patterns of seed density fluctuations (Solbreck & Ives, 2007; Solbreck & Knape, 2017).

Lygaeus equestris populations in the study area (and in Sweden) are evidently enemy-free! Whereas Mediterranean *Lygaeus* spp. populations are known to harbour both tachinid flies attacking adults and egg parasitic wasps (Anderson, 1991), no such parasitoids attacking *L. equestris* have been found in Sweden. Nor have any cases of predation on *L. equestris* been observed (CS 50 years of field work).

2.2 | Data collection

The abundances of *V. hirundinaria* fruit and of *L. equestris* adults were measured every year in every plant patch 1977–2012. Populations of *L. equestris* were estimated by mark-recapture during two phases of the life cycle. First, in June during the start of the oviposition period, and second in late August to early September when most bugs of the new generation had become adults but before the autumn flights to overwintering sites had commenced (Figure 2). Bugs were marked with a felt-tipped marker pen (Figure 1b,c). All bugs in a patch had the same marking pattern, but marks were unique to each patch (a check on movements). Equal proportions of the sexes were marked and recaptured (CS unpublished data).

FIGURE 1 (a) A part of one of the 32 patches with the host plant *Vincetoxicum hirundinaria*. Flowering plant tufts can be seen growing along the rock crevices. (b) The late Birgitta Tullberg marking bugs at Tullgarn (around 1980). (c) Adult *Lygaeus equestris* (with a mark on the left side of the thorax indicated by arrow) basking on a host plant leaf. (d) Aggregation of overwintering bugs in a rock crevice (e) Last instar nymph sucking on an old *V. hirundinaria* seed on the ground.



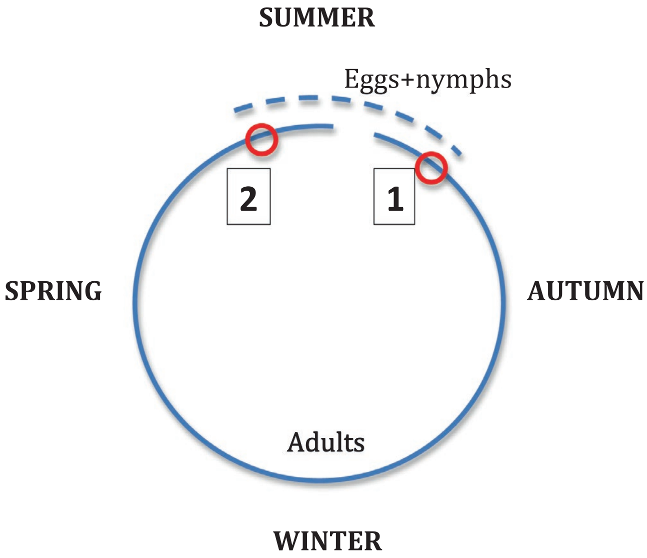


FIGURE 2 Life cycle of *Lygaeus equestris*. Most eggs are laid in June–July and nymphs occur until September. Circles indicate sampling occasions namely (1) adults *before* autumn migration (usually in late August to early September) (end of "summer" period) and (2) adults in host plant patches *after* the spring migration at the start of the oviposition period (usually in the middle of June) (end of "winter" period).

Two visits were made for each period and patch. On the first visit, the patch was traversed and all bugs found were marked and counted. The second visit was normally made later the same day or on the next day. Then all unmarked and previously marked bugs found were counted. Visits were planned to provide ample time for mixing of marked and unmarked individuals but also to minimize risks of flights in and out of patches. During the second period, last instar nymphs were counted. Thus, a ratio of nymphs to adults could be calculated, see below.

Usually, all *V. hirundinaria* fruit were counted in all patches at the end of the summer, but in years with very high fruit densities, fruit were only counted in a subsection of the larger patches and the count area multiplied by total patch area. In years with low to medium fruit density, all fruit were non-destructively checked for the presence of *E. connexa* larvae. In years with high fruit density, samples of fruit were taken in the larger patches (most samples were in the range 200–600 fruit). For further details on seed and *E. connexa* monitoring see (Solbreck & Knape, 2017).

Our study did not require ethical approval, nor did it need any permission for field work.

2.3 | Factors potentially affecting *L. equestris* populations

2.3.1 | Weather factors

Sun-basking is a prominent behaviour in *L. equestris*. It allows the insect to quickly raise its body temperature far above the ambient air temperature. This has a strong positive effect on egg production (up to about 30°C) (C Solbreck unpublished data), and on the ability of the insect to take off and fly (Solbreck, 1976). Accordingly, *the number of sunshine hours* during the summer months June+July or June+July+August has proven to be a better predictor for population change than air temperatures (Solbreck, 1995).

Effects of winter weather conditions are less well understood. We used *winter minimum temperature* as very low temperatures may cause freezing of the insects. Additionally, snow cover may influence survival by insulating against cold or desiccation or affect possibilities for sun-basking at the end of the over-wintering period. We therefore also use the variable "duration of the period with snow-covered ground". All weather data refer to the standard meteorological station in Stockholm about 50 km north of the study area.

Correlation between weather variables was generally low except for between winter temperature and number of snow days (rho = −0.5) and between sunshine hours in June and July and sunshine hours in June, July, and August (rho = 0.9). The two measures of sunshine hours, however, enter different parts of the analysis below (winter and summer dynamics) so that the correlation does not pose issues.

2.3.2 | Food web interactions

Previous analyses of data from the first 18 years of this study (Solbreck, 1995) as well as field experiments (Solbreck & Sillén-Tullberg, 1990) showed that food resources can limit *L. equestris* populations in some years. We use *the total* number of seed pods of the host plant as a measure of resource abundance. In an additional analysis, we also use the proportion of seed pods not attacked by *E. connexa* to investigate potential resource competition. Natural enemy effects are assumed to be negligible, see above.

2.4 | Overview of modelling approach

We modelled the dynamics of the whole population at Tullgarn using a state-space model to take sampling error into account. To reduce computation time, this was done in two steps. In the first step, we estimated the total population size at Tullgarn in early and late summer using mark-recapture data in a hierarchical sampling model.

In a second step, we took the estimated distribution of the total population sizes from the first step as input to a Bayesian population state space model. The state-space model includes a population process as well as a measurement process with the aim of filtering out noise to better capture population dynamics. For the state-space model, we approximated each of the posterior distributions of the annual total population sizes obtained in the first step with gamma distributions. These gamma distributions were then given as input data to the state space model to account for uncertainty in the estimate. The approximation ignores correlations among population size estimates at different times, but these are overall small (average absolute value of posterior correlation = 0.03) and ignoring them results in substantial computational gains.

2.4.1 | Sampling model

We fitted models separately to data from the two periods (early summer and fall), but both had a similar structure. We used mark-recapture data from the two visits at each patch as the main input to the model. We also included a correction factor for immature individuals encountered in the fall sampling period. The model included patch and time effects, and patch and year specific abundances were modelled with a negative binomial distribution. The posterior distributions of abundances summed over all patches in each year were used as estimates of total population size and used as input to the state-space model. Further details of the sampling model can be found in Supporting Information S1.

2.4.2 | Population state-space model

For the population model, we used Gompertz type dynamics in a state space formulation. Denoting the latent population size in early summer in year t by n_{1t} and the latent population size in late summer by n_{2t}, our model for summer dynamics is

$$n_{2t} = n_{1t}\ \exp\left(a_0 + a_1\,sunJJ_{1t} + a_2\ \log\left(fruit_{t-1}/n_{1t}\right) + \varepsilon_t\right) + I_1$$

where $sunJJ_{1t}$ is the number of sunshine hours in June and July, $fruit_{t\text{-}1}/n_{1t}$ is the number of fruits in year $t-1$ per adult in early summer of year t intended as a proxy for resource availability, and ε_t is a zero mean normal residual term with standard deviation σ representing process error in the summer dynamics. The last term I_1 is a parameter representing immigration of individuals from outside the study area. It is assumed fixed between years. The term with fruit resources per adult determines intrinsic density dependence, and the parameter a_2 determines the strength of this dependence. When a_2 is positive, there is negative density dependence, and the population is regulated. Strong compensatory regulation occurs when a_2 is close to 1. In a separate analysis, we also add the log-transformed proportion of seeds attacked by *E. connexa* as a predictor in the above model to investigate the effects of resource competition.

Similarly, our population model for the winter dynamics is

$$n_{1t} = n_{2t-1}\ \exp\left(b_0 + b_1\,temp_t + b_2\,snowdays_t + b_3\,sunJJA_{t-1} + \eta_t\right) + I_2$$

where $temp_t$ is the minimum temperature in the winter between year $t-1$ and t; $snow\text{-}days_t$ is the number of snow-days in the winter between year $t-1$ and t; $sunJJA_{t\text{-}1}$ is the number of sunshine hours in June, July and August of year $t-1$; and η_t is a zero mean normal residual term with standard deviation τ representing process error in the winter dynamics. As for the summer dynamics, we also include the parameter I_2 to represent immigration.

As mentioned above, observation error is incorporated by plugging in the estimated gamma parameters for each year and session (early and late summer). Specifically

$$r_{it} \sim \mathrm{Gamma}\left(s_{it}, n_{it}\right)$$

where r_{it} and s_{it} are the gamma rate and scale parameters estimated from the posterior distribution of the $N_{i\text{-}t}$ (by matching means and variances) of the sampling model for session i (1 or 2) and year t.

We fitted the model using the software JAGS (Plummer, 2003), running 10,000 MCMC iterations. All r-hat values were less than 1.02, indicating sufficient convergence. We used normal priors with mean zero and variance 1000 for intercepts, normal priors with mean zero and variance 100 for covariate coefficients, exponential priors with rate 2 for process error standard deviations, and exponential priors with rate 0.1 for the number of immigrants.

2.4.3 | Changepoints

In addition to analyses of dynamics, we also used basic changepoint detection methods to check if there was statistical evidence for changes in the mean or variance of seed production and in bug abundances (using point estimates of abundance). We also checked for changes in the mean and variances of log transformed seed numbers and bug abundances. We used the functions cpt.mean and cpt.var. functions from the changepoint package with default settings, checking for a single changepoint (Killick & Eckley, 2014). These methods assess the evidence for the existence of a break in the data such that the mean or variance differs between the periods before and after the changepoint. The results are intended as indicative to complement visual patterns, not as definite evidence for regime shifts.

3 | RESULTS

3.1 | Fluctuation patterns

Fluctuations in the abundance of seeds and insects were very large; the range being almost four orders of magnitude (Figure 3). Patterns of fruit and insect fluctuations are different. Seed resources exhibit rapid fluctuations, whereas the insect population shows slower dynamics. The positions of peak seed densities are not like insect peak densities, which tend to coincide with minima in seed density. This results in extreme fluctuations in per capita seed resources. There is also a tendency towards higher peaks in both resource and insect densities towards the end of the study.

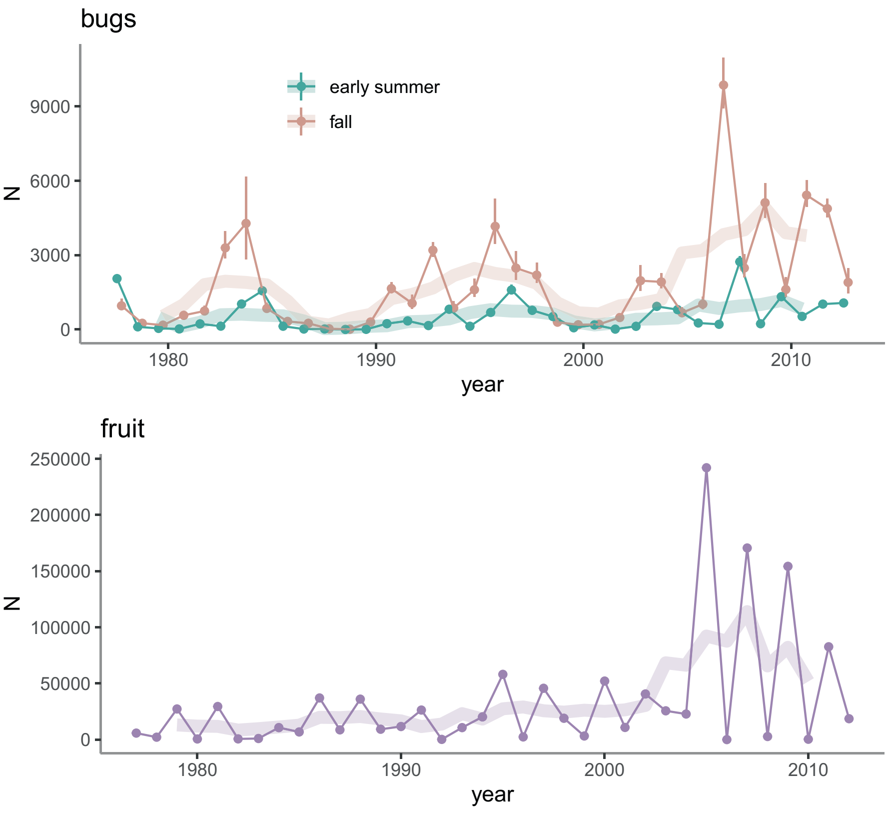


FIGURE 3 Number of *Lygaeus equestris* adults before (red) and after (green) overwintering (top panel), and number of fruit set by the plant (purple, bottom panel). Thick lines denote 5-year running means.

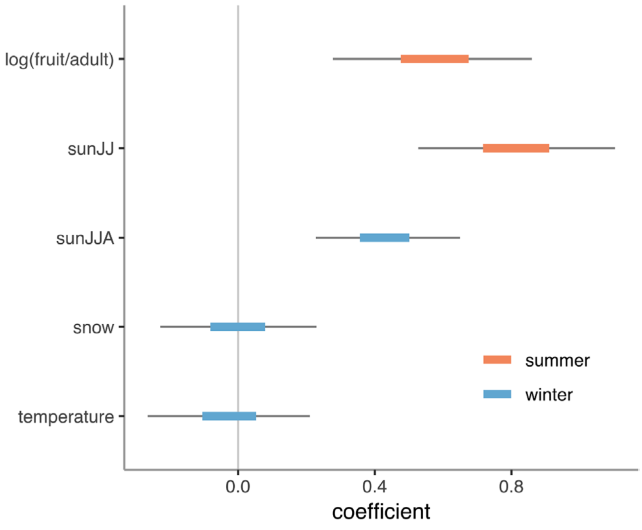


FIGURE 4 Estimates of coefficients for standardized model factors. Thick lines show 50% and thine lines 95% credible intervals.

3.2 | Analysis of dynamics

Based on the choice of environmental factors motivated and listed in the materials and methods section, we analysed the role of environment and insect density using the population state-space models capturing summer and winter dynamics.

For summer growth rates, model estimates suggest both direct and indirect effects of weather (Figure 4). The direct effect comes from a strong association with the number of sunshine hours during the early and middle part of the summer (June plus July). The indirect effect comes from an association with per capita seed resources expressed as the number of seeds in the previous year per adult present in early summer. While per capita seed resources are strongly associated with summer growth rates (Figure 4), the corresponding density dependence points to weakly regulated dynamics with the coefficient $a_2 = 0.2$ (95% credible interval: 0.1, 0.3).

For winter growth rates, the model estimates suggest direct effects of weather through an association with the number of sunshine hours during the preceding summer (June, July, and August). There were no clear associations between winter minimum temperature or number of snow-days and winter growth rates.

The model with all seeds (un-attacked + attacked by the seed predator *E. connexa*) produced nearly identical estimates to the model with all seeds as well as the proportion of un-attacked seeds, and there was no clear effect of the proportion of un-attacked seeds in the latter model (Supporting Information S1, Figure S1).

While there are large process errors due to the large fluctuations in population size, the model explains a large proportion of the variance. For summer growth rates, the process error standard deviation is large, 0.8 (0.6, 1.0) (posterior mean + 95% credible interval), but a large proportion of the variance is captured by the model, 70% (50%, 80%). Winter growth rates have a lower process error point estimate, 0.6 (0.4, 0.7), and the model captures a moderate proportion of the variance, 40% (20%, 60%).

To investigate the consistency of effects of environmental covariates and resource availability during the study period, we estimated the dynamic model using subsets of the data with years excluded in

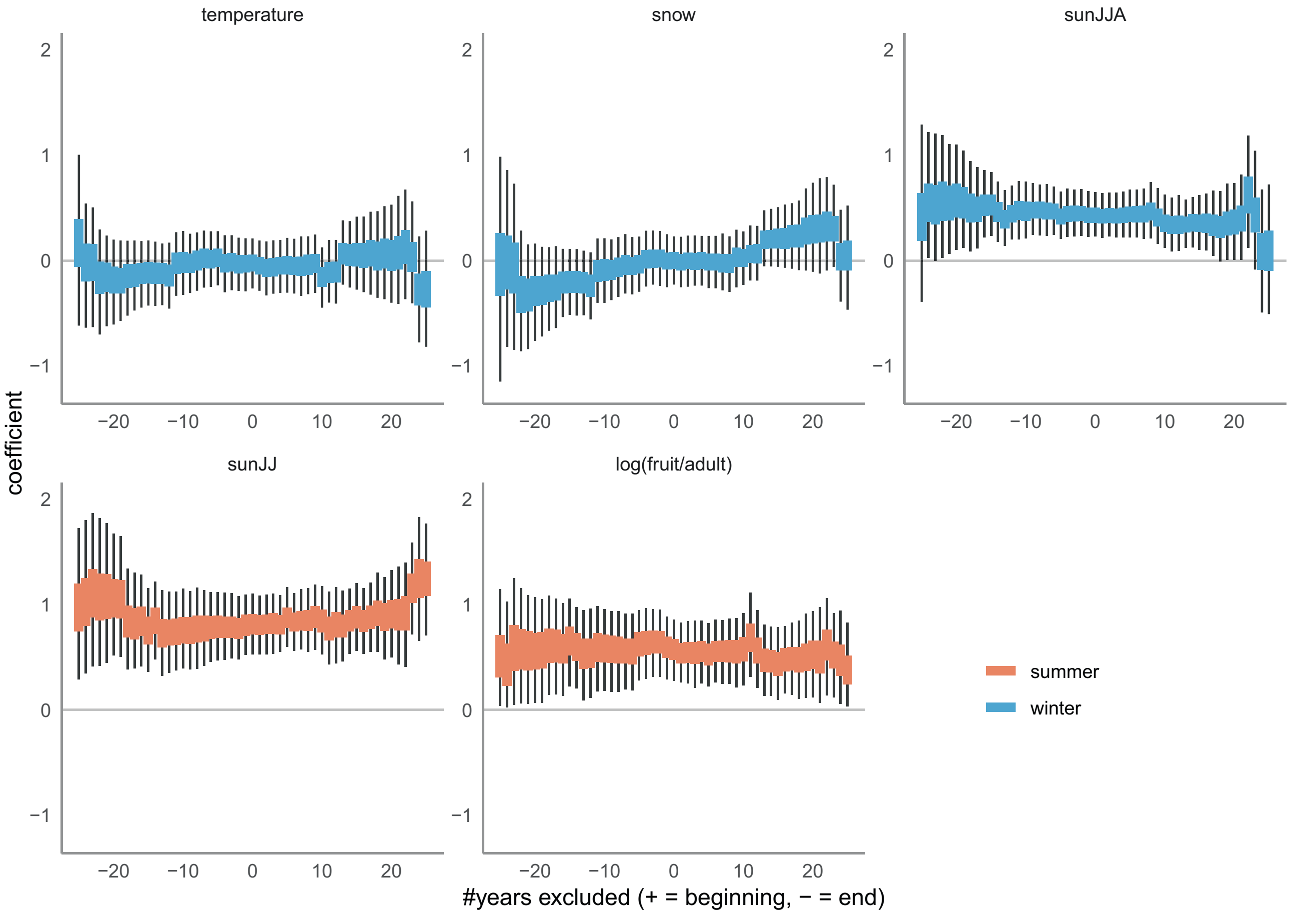


FIGURE 5 Parameter estimates using subsets of the data with years excluded in either the beginning (positive values) or end (negative values) of the study period. Thick lines show 50% and thine lines 95% credible intervals. Thick lines show 50% and thine lines 95% credible intervals.

either the beginning or end of the study period (with a minimum of 10 years included). We examined how parameter coefficients of the dynamic model changed because of the exclusions (Figure 5). While point estimates of some parameters differed depending on whether years were excluded in the end or the beginning, when considering parameter uncertainty, there was no clear evidence for a directional change in parameter estimates. For the parameters with the strongest effects (sunshine hours and fruit availability), parameter estimates were largely stable with respect to the time period, with a few exceptions for very short time periods (i.e. most years excluded).

There were no obvious changes in model residuals across time (Figure 6). First-order autocorrelation of point estimates of the residuals was 0.4 for summer dynamics and 0.2 for winter dynamics. For the summer dynamics, this suggests the potential presence of additional structure not captured by the model. Accounting for this autocorrelation in the model residuals via an AR1 process resulted in only negligible differences in parameter estimates.

3.3 | Changepoints

The changepoint analyses of the mean and variance of seed production both identified a change between 2004 and 2005, supporting the visual pattern in Figure 3. For bugs, a change in the mean between 2006 and 2007 was identified for early summer abundance, and between 2005 and 2006 for fall abundances. No changes in the variances of bug abundances were identified. When log transforming, no changepoints were detected in seed production, while a change in mean log abundance between 1989 and 1990 was identified for both the early summer and the fall population.

4 | DISCUSSION

4.1 | Overview

Our results show that the *L. equestris* population is mainly influenced by direct weather effects and by its main seed resource that is in turn influenced by weather at multiple time scales (Solbreck & Knape, 2017). These conclusions are in line with those of a previous study before the change in resource dynamics (Solbreck, 1995), showing that the drivers of dynamics of the population seem to have been largely unaffected by the change in resource dynamics. In terms of patterns of fluctuation, the full study indicates that changing patterns of seed production, entering a bi-annual seed set pattern with high peaks in the latter part of the period

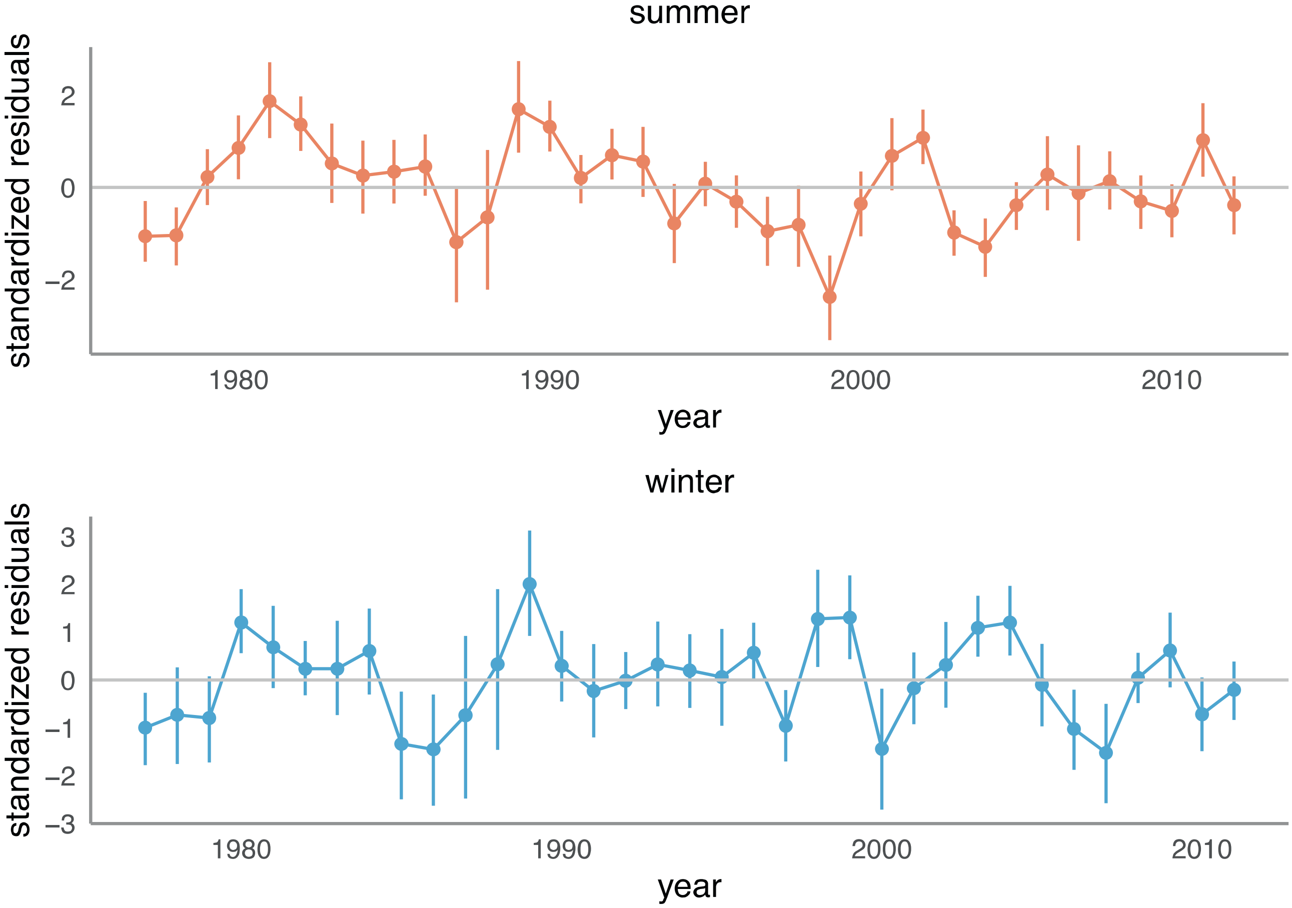


FIGURE 6 Posterior distribution of state-space model residuals (ε_t and η_t divided by standard deviation) for summer and winter dynamics.

(Solbreck & Knape, 2017), have led to higher abundance levels of the bug but do not appear to have otherwise caused large changes in its dynamics. This suggests an example where drastic changes in food resource variability, presumably induced by climate change and a longer growing season, transfer to changes in mean consumer abundance without clear effect on consumer variability or on driving mechanisms behind dynamics.

4.2 | Direct weather effects

The statistical evidence for direct effects of summer weather on the population can be directly linked to individual behaviour and physiology. By moving in and out of sunlit spots, *L. equestris* can thermoregulate behaviourally in sunny weather (Solbreck, 1976), which is important in the cool Swedish climate. The more sunshine hours during the summer, the longer optimal body temperatures can be maintained, resulting in more eggs being laid and more nymphs surviving to adulthood. This behaviour also explains the delayed effect of sunshine conditions on winter survival. A sunshine-deficient summer causes slower development of immatures, leaving less time to accumulate fat reserves essential for overwinter survival of adults (Solbreck, 1972).

Many insect populations are directly affected by winter weather conditions. For example, the effects of snow cover on egg survival (Roland et al., 2021), snow-melt dates on larval/pupal survival (Boggs & Inouye, 2012), and temperature lows on egg mortality and phenological mismatch (Büntgen et al., 2020). We found no statistical evidence for snow cover conditions or low temperatures affecting the survival of overwintering *L. equestris* bugs. However, there was more unexplained variation in population change during the winter than during the summer period.

4.3 | Indirect weather effects and resource variability

Large fluctuations in seed availability usually put their mark on the dynamics of the seed-seed predator link (Crawley, 2014; Holland et al., 2015; Hulme, 1998; Janzen, 1971; Kelly & Sork, 2002; Linhart et al., 2014; Solbreck & Ives, 2007; Solbreck & Knape, 2017), and they also dominate the trophic web interactions of *L. equestris*. The effect of seed resources implies indirect effects of weather on the insect at multiple temporal scales. At a relatively short scale, seed production has been shown to be associated with weather. Combined rainfall in June and July is coupled to higher seed pod density of the present year (Solbreck & Knape, 2017), and experimental watering also resulted in more seed pods produced both in the present and the succeeding year (Ågren et al., 2008). As seeds on the ground from the previous year form an important resource for the bug (Figure 1e), this implies a further one-year delayed effect on the bug population. At a longer scale, growing conditions have improved, resulting in larger patches of *V. hirundinaria*, suggesting a slow long-term non-stationary component of seed production, probably an effect of a warmer climate causing an extended growing season (Solbreck, 2012; Solbreck & Knape, 2017). The onset of bi-annual seed set with high peaks, also potentially a consequence of climate change (Solbreck & Knape, 2017), adds further to the complexity of weather effects on the bug, see below.

4.4 | Competition

Interspecific competition for food appears to be unimportant for *L. equestris*. The most likely candidate for competition is the larva of the tephritid fly *E. connexa* that feeds on developing seeds of *V. hirundinaria*, often attacking a high proportion of seed pods (Solbreck & Ives, 2007; Solbreck & Knape, 2017). However, we found no evidence for it competing with *L. equestris* as models using all seed pods (attacked + un-attacked by *E. connexa*) provide similar results to models only considering un-attacked pods (Supporting Information S1), due to a high correlation between the two measures. Other phytophages on the host plant (see material and methods) are uncommon in relation to their food resource and unlikely to have any effect.

4.5 | Geographical limitation

It should be noted that the present study pertains to a Swedish population of *L. equestris*, which is on the NW fringe of a wide geographical species range (Aukema & Rieger, 2001). Mechanisms of population change in insects often vary geographically (Bonsall et al., 2003; Mills et al., 2017; Nice et al., 2018), and this is also the case in *L. equestris*. In southern Europe, for example, the trophic web of *L. equestris* is very different, with several coexisting Lygaeinae (subfamily of *L. equestris*) species sharing a parasitoid guild attacking eggs and adults. This provides a basis for rather complicated trophic interactions (Anderson, 1991; Solbreck, 1995).

4.6 | Implications for population dynamics

One might expect that the variability in the dynamics of the insect should have changed because of these new patterns in seed production initiated in 2005. Insect abundance did reach its overall largest numbers in the fall of 2006, when plentiful resources were available due to the abundant seed production in 2005, and insect abundance levels (at least in fall) also were generally higher after this change. However, we did not find clear evidence for a corresponding change in variability of the population, and neither model coefficients nor residuals suggest any clear change in its dynamics. The population therefore seems to have reacted to the new pattern mainly through higher abundance, without entering any new dynamic regime and leaving no clear trace in its inter-annual fluctuations. This is in contrast with a previous study of effects of changing patterns of environmental variability on insect dynamics (Pepi et al., 2021) that suggested that the dynamics after an environmental shift could not be understood from an analysis of the dynamics before the shift. Our study therefore offers more hope of understanding insect responses to a changing climate, at least in simple food webs and given that knowledge of mechanisms is available.

Under our population model, the factors influencing growth rates can be partitioned into a negative density dependent effect and effects from weather and seed production (Figure 4), which are autocorrelated. Roughgarden (1975) analysed the implications of such autocorrelated external factors for the type of model used here and showed that the response of a population depends on the parameter for the strength of density regulation (determined by the parameter a_2, corresponding to the parameter r in Roughgarden (1975)). With weak regulation as estimated from our model, small amounts of environmental variation can cause large variation in abundance. The model further acts as a low-pass filter of the external factors, meaning that short-term fluctuations in them will not carry over to the population trajectory (Laakso et al., 2001). With the weak regulation, the large variation due to weather effects, variation in seed production dynamics, and unexplained variation will therefore contribute to large unstable fluctuations in the population. This provides an explanation for why the sudden onset of changed variability in seed production patterns around 2005 did not result in obvious changes in variability in the bug population.

On the other hand, the slow indirect effects of weather from an increasing plant population as well as climate related long-term effects of weather have a greater potential to 'survive' the low pass filter and leave persistent marks in population trajectories, which is in line with the higher fall abundance in the period after the onset of bi-annual seed set in 2005. In the same way as for indirect effects via seed production, short-term inter-annual weather variation will also not leave strong marks in the population trajectory.

Our long-term population study illustrates the complex nature by which weather affects insects, operating both directly and indirectly, and at multiple time scales even in a very simple food web. It adds to a growing number of studies demonstrating the variable ways in which weather influences insect populations (e.g. Azerefegne et al., 2001; Boggs & Inouye, 2012; Hambäck, 2021; Matter et al., 2011; Solbreck et al., 2022). How such complexity among drivers of population growth affects population variability depends critically on the form of density dependence (Roughgarden, 1975). With relatively weak regulation, the response to short-term resource variability is slow, leading to substantial long-term fluctuations in the population but without clear traces in its short-term variation. This emphasizes that responses to even drastic changes in resource dynamics, for example induced by climate change, can be subtle and hard to detect without accurate long-term data and knowledge of mechanisms.

AUTHOR CONTRIBUTIONS

Christer Solbreck conceived the ideas, designed the work and collected the data for the field study. Jonas Knape developed the statistical analysis. Both authors contributed equally to the interpretations of analyses and the development of the paper.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3r2280gtb.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Additional details of sampling model.

Figure S1. Comparison of model coefficients under the main model with a coefficient for the (log transformed) number of fruits per adult (left), and a model with an extra coefficient for the (log transformed) proportion of unhealthy fruit (right).

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