Temperature and precipitation are two major factors determining arthropod population densities, but the effects from these climate variables are seldom evaluated in the same study system and in combination with inter- and intraspecific density dependence. In this study, I used a 19 year time series on plant variables (shoot height and flowering incidence) and insect density in order to understand direct and indirect effects of climatic fluctuations on insect population densities. The study system includes two closely related leaf beetle species (*Galerucella* spp.) and a flower feeding weevil *Nanophyes marmoratus* attacking the plant purple loosestrife *Lythrum salicaria*. Results suggest that both intraspecific density dependence and weather variables affected *Galerucella* population densities, with interactive effects of rain and temperature on insect densities that depended on the timing relative to insect life cycles. In spring, high temperatures increased *Galerucella* densities only when combined with high rain, as low rain implies a high drought risk. Low temperatures are only beneficial if combined with little rain, as high rain cause chilly and wet conditions that are bad for insects. In summer, interactive effects of rain and temperature are different because high temperatures and little rain cause drought that induce wilting in plants, thus reducing food availability for the leaf feeding larvae. In contrast, the density of the flower feeding weevil was less affected by temperature and precipitation directly, and more indirectly interspecific density dependent effects through reduced resource availability caused by previous *Galerucella* damage.

Keywords: density dependence, *Galerucella*, *Lythrum*, *Nanophyes*, population dynamics, precipitation, temperature

**Introduction**

Understanding temporal fluctuations in species density is a major task of ecological research, where variation in climate and density dependence are two major driving forces explaining population abundance and fluctuations (Cappuccino and Price 1995, Turchin 2003). Fluctuations in temperature, precipitation and other climatic variables seem to be of particular importance for determining fluctuations in...
arthropod populations, because of the climatic sensitivity of many arthropod life-stages (Azerefegne et al. 2001, Solbreck and Ives 2007). The debate concerning the role of density dependent population regulation, inter- or intraspecific, and density independent effects such as climate as predictors for population density and fluctuations has deep roots in ecological research (Nicholson 1933, Elton 1949, Andrewartha and Birch 1954, Turchin 1995), and understanding these processes is important not only for fundamental research but also for developing improved predictions for arthropod responses to climate and other environmental factors. Yet, climate, inter- and intraspecific, density dependence are typically not evaluated simultaneously in attempts to understand population fluctuations and density in arthropods (but see Azerefegne et al. 2001).

Climate not only affects life history traits directly, but also indirectly because climate factors affect the strength of species interactions (Öhlund et al. 2015, Uszko et al. 2017, Toftegaard et al. 2019), or because climate effects modulate the strength of interspecific density dependent effects through chains of trophic interactions (Tylianakis et al. 2008, Binzer et al. 2012, Zhang et al. 2017). Englund et al. (2011) showed for a range of predator and prey types that maximum intake rates and attack rates typically have an optimum, and these effects would presumably translate to changes in population dynamics (Uszko et al. 2017). The causes for these climate related effects on trophic interactions are not always clear but may arise because of changes in specific demands of predator individuals, such as changes in the nutritional requirements, body size or hunting capacity (Binzer et al. 2012, Öhlund et al. 2015), changes in prey traits, such as nutritional quality (Coley 1998, Zvereva and Kozlov 2006, Cornelissen 2011) or mismatches in phenological appearances (Russell and Louda 2005, Kharouba et al. 2018). Yet, we lack empirical data concerning how such climate effects on population dynamics of one species is filtered through inter- or intraspecific density dependent effects, and the only studies this far of long-term effects are from simulation models (Bascompte et al. 2019).

A complicating aspect when studying climate effects on population abundance and dynamics is that timing is important, but also that these dynamics are affected by multiple factors as well as by interactions between factors. For instance, high temperatures during spring may lead to accelerated plant growth rates whereas high temperatures during summer may lead to drought and reduced growth rates (Nicôle et al. 2011), creating potentially counteracting effects from a warmer climate. Similarly, precipitation may have quite different effects on population growth during cold and warm temperatures. It is therefore important to also account for variations between seasons and how weather variables during different parts of the year may be positively or negatively correlated.

This study quantified the direct and indirect effects of temperature and precipitation on the dynamics of insects attacking the perennial plant purple loosestrife *Lythrum salicaria* using a long term (up to 19 years) data set involving 29 populations situated in a 245 km gradient along the Baltic Sea shore in Sweden. Purple loosestrife in this area is native and plants are strongly affected by herbivory, both from leaf-feeding beetles (*Galerucella* sp.) that may completely defoliate the plant and thereby reduce plant growth, flowering and seed set (Katovich et al. 2001, Lehndal et al. 2016) and from roedeer *Capreolus capreolus* grazing that cause complete removal of aboveground plant biomass. Because effects on plant traits is strong from both beetles and roedeer, I hypothesized that herbivory from these species may affect insects feeding later in time on purple loosestrife, such as a flower feeding weevil *Nanophyes marmortatus*, but also that weather effects on Galerucella densities may cascade to affect Nanophyes densities. To analyze direct and indirect effects in this system, I first identified total effects of temperature and precipitation on plant variables and insect densities, and then separated direct and indirect effects, mediated through intra- and interspecific density dependence, using a structural equation model based on expected density dependent effects (Fig. 1b).

**Methods**

**Study species**

*Lythrum salicaria* is a common shoreline plant more or less along the entire Baltic Sea shoreline but also occurs in inland wetlands and ditches in southern Sweden. The plant is perennial, and occurs widely in Eurasia and as an invasive plant in North America and elsewhere (Blossey et al. 2001). The plant is attacked by a range of monophagous chrysomelid and weevil species, where the most common leaf feeding species include *Galerucella calmariensis* and *G. pusilla*, whose larvae may reach very high densities and completely defoliate the plant (Hambäck et al. 2000, Katovich et al. 2001, Lehndal et al. 2016). Live individuals of the two species are difficult to separate except as larvae; *G. calmariensis* larvae have a rich yellow color and *G. pusilla* larvae are more whitish-yellow (Fors et al. 2014).

In sites on the Baltic Sea shore, *Galerucella calmariensis* is by far the most common species but *G. pusilla* occasionally dominates on soft-bottom shore sites. Their life cycles are similar (Fig. 1a); overwintering as adults, emerging in spring (May in the study area), egg-laying in early summer (June in the study area), larval feeding on leaves, stems and flowers during summer and thereafter pupation in the ground. The third common species on *L. salicaria* in the area is the weevil *Nanophyes marmortatus*. Members of this species emerge in mid-June, mate on the plant and lay eggs on flower buds in late June and early July. Larval development and pupation occur within a single flower bud during July and early August before overwintering as adults. While I focus here on *Galerucella* and *Nanophyes*, several other species were observed on *Lythrum salicaria* over the years, such as the root feeding weevil *Hylolobius transversovittatus*, the stem-galling weevil *Nanomimus circumscriptus* and the flea beetle *Lythraria salicariae*, which are all monophagous on *Lythrum* in the area. The root feeding weevil was only...
occasionally found in the surveys but is harder to detect and may be overlooked. The stem-galling weevil is easier to detect due to the conspicuous gall that often bends the stem, but this species only began to appear in two sites in 2011. Other herbivore species include the common spittlebug *Philaenus spumarius*, and the only predator occurring abundantly on *L. salicaria* plants during the study was the common lacewing *Chrysoperla carnea*. Ladybird larvae *Coccinella septempunctata* were common in one site in one year, and then seemingly reduced *Galerucella* egg and larval densities considerably (see also Hambäck et al. 2000), whereas other ladybird species only occurred sporadically. The *Galerucella* larvae were also attacked by a parasitic wasp, *Asecodes parviclava* at low rates (typically less than 10%). For unknown reasons, parasitism rates are much higher in areas further north (Fors et al. 2016), possibly due to the presence of an alternative host (Stenberg et al. 2007).

**Field sampling**

Field data were collected annually, at the end of June, in 29 populations in a 245 km gradient along the Baltic Sea shoreline during the period 2000–2018 (Fig. 2, Supporting information), with some variability in the starting and ending of time series. Site selection was mainly based on accessibility and that the sites had a sufficiently large *L. salicaria* population (> 100 individuals). Site characteristics were variable, with some sites having fairly soft-bottom shores, covered by silt or sand, to medium rocky areas, where small rocks and vegetation was interspersed, to areas with large rocks, with

![Field sampling](image-url)
vegetation in between rocks and finally to cliff-dominated shores, where plants mainly grow in narrow crevices with little soil (Supporting information). Site exposure varied from sites situated in protected bays to sites more exposed to wind and waves. Among sites, there was some variation in the vegetation composition but major plants include, in addition to *L. salicaria*, a range of common shoreline forbs (e.g. *Lysimachia vulgaris*, *Filipendula ulmaria*, *Artemisia vulgaris*, *Angelica sylvestris*, *Valeriana sambucifolia*) and grasses (e.g. *Agrostis stolonifera*, *Festuca rubra*).

Within each population, I surveyed all insect species on 56 randomly selected *L. salicaria* shoots along transects. Randomization was repeated each year and I did not mark or follow shoots between years. On each shoot, I counted all insects (egg, larvae and adults), measured shoot height (cm) and flowering incidence at the shoot level. Early in the study, I observed that roe deer *Capreolus capreolus* frequently consumed *L. salicaria* shoots on the shoreline. Roe deer removed the whole shoot, leaving only very small stumps, and I used the incidence of cut shoots as a measure of this consumption. The focal insect species were *Galerucella* spp. and *Nanophyes marmoratus*. *Galerucella* densities were estimated as egg counts per shoot, rather than as counts of adults or larvae, the reason being that adult and larval densities showed much larger variations within years caused by a lower detectability whereas egg densities were more stable measures of population size. To estimate the maximum egg density, counts were made towards the end of the egg laying season (late June, Fig. 1a) and before hatching. In some rare cases, during exceptionally warm spring years, hatching had started at the sampling time in some sites, which made egg counts less precise (though egg numbers can be counted shortly after hatching). I noted these cases to control for deviations in the statistical analyses, but they were sufficiently rare not to affect any conclusions. A disadvantage with egg counts is that the *Galerucella* species cannot be distinguished based on egg characters, but independent estimates suggest a strong dominance of *G. calmaris* in the study area. Among other insects, I counted adults of *N. marmoratus* and most other species, with the exception of lacewings where counts include larvae and eggs. Insects other than *Galerucella* and *Nanophyes* were too rare for analysis and are not included here.

During field data collections, it was apparent that four populations (no. 24 – no. 27, Fig. 2), that were all situated on one island, showed drastic reductions (> 90%) in both *Galerucella* and *Nanophyes* densities connected to a strong increase in roe deer grazing on the host plant. Already in 2007, *Galerucella* densities in these populations had been reduced to less than 10% of the mean value before 2006 and thereafter stayed low until 2010, when I decided to end sampling of these populations. Because these reductions caused time series to be strongly non-stationary, these four populations were excluded from further analyses of insect dynamics leaving 25 populations in the analysis.

To estimate climate factors for each site, I used data on hourly temperatures and daily precipitation recorded from the closest available SMHI weather station (<www.smhi.se>) that was located sufficiently close to the shore to resemble the climate at the study sites (Fig. 2). From the weather data, I extracted mean temperatures (°C) and total precipitation (mm) for May, June and July respectively. The focus on these time periods is motivated based on insect life cycles. Adults of *Galerucella* appear in May, lay eggs in June whereas larval development occurs in July. Similarly, adults of *Nanophyes* appear and lay eggs in late June to early July, and larval development occurs in July. Because the number of weather stations is much smaller than the number of sites, multiple sites include the same climatic data. However, the focus of the analyses was on between year variation with site as random intercept and where absolute differences between the study site and the connected weather station therefore is less important for understanding the patterns.

**Statistical analyses**

Because the data set consists of a large number of parallel time series data, were analyzed with linear mixed effects models with site as a random effect using the package nlme (Pinheiro et al. 2009) (for hypothetical model see Fig. 1b). In order to separate direct and indirect effects of climate, I used an approach where relevant time scales and climate variables were first selected using the dredge function in MuMln (Barton 2019) and then combined with biological variables and site characteristics in a piecewise structural equation model (SEM, Lefcheck 2016) to explain temporal and spatial variation in insect densities and plant variables. To identify relevant time scales and climate variables in the first step, I modelled each response variable (*Galerucella* egg density, *Nanophyes* adult density, shoot height, flowering incidence) as a function of previous years density (up to a lag of two years) and shoot height respectively, and all climate factors and their two way interactions (temperature and precipitation for May, June and July, where precipitation was ln-transformed to normalize the distribution). Because insect densities and plant variables were estimated at the end of June, climate factors for May and June were included from year (t) whereas climate factors for July were included from year (t − 1).

To separate direct and indirect effects of weather variables in the second step, I constructed an initial SEM-model based on climate variables from the first step, expected interactions of biological variables (as indicated in Fig. 1b) and site characteristic. Due to the lower sample size for site level characteristics, I only included one characteristic for each response variable in the SEM. The SEM combined four individual mixed effects models (lme), each with site as random variable, for the different response variables (*Galerucella* egg density, *Nanophyes* density, shoot height, flowering incidence) using the psem command in the piecewiseSEM package (Lefcheck 2016). This initial model was assessed with a D-separation test, to detect missing links, and the overall model was tested with Fisher’s C statistics where a non-significant p-value indicates a good fitting model. Non-significant links were removed until AIC was minimized. To account for correlation structures caused by
lag effects, correlated errors were included between some predictor variables. To better illustrate the intraspecific density dependence graphically, I also calculated rates of change (ln(density in year t + 1/density in year t)) for *Galerucella* and *Nanophyes* densities. All analyses were performed in R 3.6.3 (<www.r-project.org>).

Finally, to examine the ability of the final model to describe the observed population dynamics, I modelled insect densities and plant variables for each site based on the parameters from the statistical models and the weather data. From these data, I calculated predicted means and coefficient of variations of each variable and compared with the observed data.

**Results**

Observed population densities and the rate of change of both *Galerucella* and *Nanophyes* varied considerably between years and sites (Fig. 3), but in some years, particularly for *Galerucella*, densities were consistently high or low across

![Graphs](image-url)

Figure 3. Yearly variation in insect densities, growth rates and plant variables (plant variables are means of 56 plants per site). The colored lines refer to site level data whereas the thick black lines refer to means across all populations.
all populations. Climate variables were also quite variable between years (Fig. 4), without a discernible trend. When calculated across all populations, temperatures and precipitation were more strongly correlated for July (mean $r = -0.44$) than for May ($r = -0.25$) and June ($r = -0.06$). Similarly, mean monthly temperatures were generally more strongly correlated between months (May versus June, $r = 0.34$; May versus July, $r = 0.40$, June versus July, $r = 0.19$) than the monthly precipitation (May versus June, $r = -0.06$; May versus July, $r = 0.24$, June versus July, $r = 0.20$).

The first step in the analysis showed that both temperature and precipitation, sometimes in interaction, affected insect densities and plant variables (Table 1), and that intraspecific density dependence only involved time lags of one year at a maximum. The trend was that cold–wet or warm–dry conditions early in the season, as well as droughts later in the season, affected insect densities negatively. First, shoot heights were positively affected by both higher May precipitation and higher July temperatures, in addition to the effect of previous year’s shoot height. Second, flowering incidences were affected by the interactive effect of temperature and precipitation for both May and June. The interactive effects of May and June weather were very similar and arose because the combination of high temperatures with low precipitation and the combination of low temperatures and high precipitation both resulted in higher flowering incidence (Supporting Figure 4).

![Yearly variation in temperature and precipitation. The colored lines refer to weather stations whereas the thick black lines refer to means across all stations. Notice the different scales for temperature in different months.](image-url)
Climate and weather are strong drivers affecting both absolute densities of arthropods as well as their temporal fluctuations, not only for this system but generally (Azerefige et al. 2001, Cornelissen 2011, Boggs and Inouye 2012, Wetherington et al. 2017). However, weather effects on species dynamics are often filtered through intra- and interspecific interactions (Solbreek and Ives 2007), and estimating the relative importance of different factors is essential for understanding changes in climatic factors on population density. In the Lythrum system, it is evident that both intra- and interspecific density dependence strongly affects the mean population density of the studied insect species. Moreover, whereas the strong intraspecific density dependence acts to dampen fluctuations, interspecific density dependence acts in this system to mediate weather effects between species, thus indirectly increasing population fluctuations. Weather effects on population densities of the leaf feeding beetles (Galerucella) early in the season seem to indirectly affect both flowering incidence and densities of the flower feeding weevil (Nanophyes) later in the season.

Several weather variables, precipitation and temperature at different time points during the life cycle, seemingly affect plant variables and insect densities both directly and indirectly. Among the most important factors seem to be conditions early and late in the life cycle, in this case May and July. Both shoot height, Galerucella densities and flowering incidence were affected by temperature and rain during May, which is the time when Galerucella adults begin to appear on plants. An interesting pattern was that the interactive effect of temperature and rain, where high temperatures combined with low precipitation and low temperatures combined with high precipitation, caused reduced Galerucella densities and increased flowering. These combinations likely represent drought conditions and very chilly conditions respectively, that may both cause increased adult insect mortality that indirectly reduced flower damage and increased flowering incidence. It is also interesting that May weather only affected Nanophyes densities indirectly, through the effect of direct and indirect effects on flowering incidence. The lack of direct effect from May weather on Nanophyes densities may occur because this species usually does not appear until June, when plants flower, and thereby avoids bad weather earlier in the spring. These results indicate that previous studies

| Shoot height (t)* | Flowering incidence (t) | Galerucella egg density (t)* | Nanophyes density (t)* |
|------------------|------------------------|-----------------------------|------------------------|
| Intercept        | 1.84 ± 0.20 (p < 0.0001) | −4.09 ± 1.04 (p < 0.0002)   | 12.4 ± 2.1 (p < 0.0001) |
| Shoot height or  | 0.31 ± 0.05 (p < 0.0001) | 0.49 ± 0.04 (p < 0.0001)    | −6.63 ± 0.04 (p < 0.0001) |
| density (t − 1)* |                        |                             | 0.31 ± 0.05 (p < 0.0001) |
| July temperature | 0.016 ± 0.007 (p < 0.03) | −0.17 ± 0.04 (p < 0.0001)   | 0.10 ± 0.04 (p < 0.02)   |
| May temperature  | 0.16 ± 0.05 (p < 0.0003) | −0.95 ± 0.23 (p < 0.0001)   |                        |
| May precipitation | 0.055 ± 0.012 (p < 0.0001) | −2.41 ± 0.60 (p < 0.0002)   | 0.23 ± 0.07 (p < 0.002)  |
| May temperature  | −0.053 ± 0.017 (p < 0.0003) | 0.27 ± 0.07 (p < 0.0003)    |                        |
| precipitation (t)* |                        |                             | 0.22 ± 0.04 (p < 0.0001) |
| June temperature | 0.25 ± 0.08 (p < 0.002)  |                             |                        |
| June precipitation (t)* | 0.66 ± 0.023 (p < 0.006) |                             |                        |
| June temperature x | −0.053 ± 0.018 (p < 0.005) |                             |                        |
| precipitation (t) |                        |                             |                        |

*In-transformed.
focusing only on temperature effects may not provide the whole picture on climatic effects on insect population densities, because higher temperatures may be beneficial during rainy spring weather and negative during dry spring weather.

Towards the end of the larval growth period, in July, it was similarly apparent that high temperatures and droughts were strongly negative for *Galerucella* densities, presumably affecting larval survival. During field work, I could observe this effect directly because a large number of plants were completely dry during the most severe drought years and thereby did not allow larval development. Even during these years, however, larger plants looked more vigorous and still flowered, which could explain why high July temperatures were not equally negative for the *Nanophyes* densities. It is likely that larger plants have deeper roots and thereby may better handle drought conditions. In addition to these effects during the reproductive and juvenile phases of the insect life cycles, it is possible that weather effects or flooding during overwintering may have reduced adult survival and affected spring population densities. Because the specific weather variable underlying survival during such a long time period (nine months) is unclear, additional experimental results would be needed to narrow the options before doing a meaningful analysis on the effect of winter weather on insect densities.

Based on these results, one may speculate on the effect from a warmer climate. If summers get hotter, the drought risk in July may increase and thereby shorten the suitable development time for *Galerucella*. On the other hand, warmer weather during the spring may enable an earlier start of egg laying, which would just change insect phenology, where the dynamic impact depends on eventual phenological mismatches (Russell and Louda 2005, Kharouba et al. 2018). However, the end result will depend also on eventual changes in precipitation during this period, that may result in shorter periods with suitable climate. Previous work on climate change effects have focused on the possibility of earlier phenology and potential increases in voltinism (Altermatt 2010). This reasoning relies on the assumption that the end of the development period is determined by reduced temperatures in the fall and not by extended droughts during summer. Droughts may also increase the spatial synchronization of populations, as previously shown for the Glanville fritillary butterfly (Tack et al. 2015), because dry conditions tend to occur over larger areas. Such effects were also apparent in our system as the synchronized population crashes observed in the time series (Fig. 2) always coincided with dry periods.

Intraspecific density dependence was strong for both insect species in this study system, and this effect was likely connected to food availability, at least for *Galerucella*, because individual plants were completely defoliated at very high *Galerucella* densities (Katovich et al. 2001, Lehndal et al. 2016). On the other hand, earlier studies show positive density dependence at low densities of *Galerucella* larvae (Hambäck 2010). This earlier experiment, however, placed all larvae on plants simultaneously in contrast to the field situation where eggs may be deposited over several weeks. When egg laying is

Figure 5. Relationships between the *Galerucella* egg density and (a) the *Galerucella* rate of change (ln(density in $t - 1$/density in $t$)), (b) *Nanophyes* rate of change, (c) flowering incidence and (d) shoot height.
more dispersed in time, small larvae, which are very sensitive
to high quality food, may appear after these resources have
already been depleted. It may then matter less that larger lar-
vae would be better able to survive on these damaged plants.

The strong intraspecific density dependence for _Nanophyes_
is perhaps harder to explain, given that their larvae only needs
a single flower for development and where the host plant typ-
ically has a very larger number of flowers. _Nanophyes_ densities
are seldom high enough to occupy a considerable fraction of
flower buds. On the other hand, _Nanophyes_ may still expe-
rience relative resource shortage because flowers are suitable
for colonization for a short time before being opened. While
the intraspecific density dependence is perhaps unclear, the
effect from _Galerucella_ on _Nanophyes_ is easier to understand,
because _Galerucella_ larvae not only feed on leaves but also on
flowers. In particular, young _Galerucella_ larvae often move
into flower buds to find a more nutritious food source during
early life but also to get protection against predation (Sebolt
and Landis 2002). It is therefore also not surprising that cli-
mate effects on _Galerucella_ densities translate to effects on
_Nanophyes_ density fluctuations. These indirect effects were
however quite weak, in contrast to what is often observed in
modelling studies (Kaneryd et al. 2012).

Whereas mean insect densities and plant variables were
well modelled by the recorded weather variables, it was
equally apparent that the statistical models strongly under-
estimated the between-year variability. This failure likely
reflects the fact that the precise connection between weather
and insect growth and mortality is yet unclear, but it is also
important to remember that the mean temperatures included
in the models do not necessarily reflect the microclimatic
conditions experienced by insect larvae and other life stages
on the plant. In the models, I used mean temperatures and
precipitation at a monthly scale but it may be that key events,
such as storms or frost, during these or other periods are more
influential than mean values. To capture these events, that
may also differ between years, is very difficult. Given the large
number of potential climatic factors, and how to estimate
them, it is likely that connections between climatic variability
and population fluctuations can only be coarsely estimated
from time series but this study nevertheless shows the type of
factors likely to be important.

An unexpected observation in this study was the role
of roedeer grazing on insect densities. I first observed this
effect on one island, where roedeer population had recently
expanded and where a very high proportion of shoots were
cut. This strong grazing almost eradicated the _Galerucella_
population and strongly decreased the _Nanophyes_ population
despite the plant population being largely intact, at least in
the short term. On the same shores, other plant species (such
as _Valeriana sambucifolia_) were also cut, even though this
damage was not quantified. It seems that roedeer move down
to the shores during nights to feed as these areas are typically
more productive than the inland pine or spruce forests, and
because the plant types growing on shores are typically more
digestible than dwarf shrubs and scattered forbs in the forest.

Similar effects of mammal grazers on insect densities have of
course been observed in other systems (Vandegehuchte et al.
2017) but they have not previously been documented on
Baltic shores.

Figure 6. Structural equation model showing direct and indirect effects of weather variables on plant variables and insect densities (for sta-
tistics of single lme’s, Supporting information). White boxes show variables varying among years and red boxes show mean values across all
years, indicating site characteristics. Black arrows indicate positive effects and red arrows indicate negative effects, where arrow width relate
to the magnitude of the coefficient standardized by the standard deviation. Blue arrows indicate interactive effects between temperature and
precipitation, that are further explained in the text and Supporting information.
To conclude, this study shows how climate and density dependence may interact to affect insect population densities, where climate factors tend to increase population variability whereas negative density dependence tends to decrease population variability. However, and most importantly, different climatic variable may interact in the effect on population growth and densities (Welti et al. 2020). In this study, we found that warm and dry conditions were positive for the leaf beetles during spring when ground water is generally more abundant, and negative during summer when water is generally more scarce. Similarly, even though wet conditions are often positive for plant and insect growth, such conditions may exacerbate effects of low temperatures. These findings strongly suggest the need to incorporate both temperature and precipitation changes in future attempts to understand effects of climate on arthropods.

Data availability statement

All data underlying the analyses in this paper (plant variables and insect densities) are available on Dryad <http://doi.org/10.5061/dryad.qz612jm4> (Hambäck 2021).

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