Title: Phenology of Insect Communities on an Elevational Gradient

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Abstract

Researchers at the Rocky Mountain Biological Laboratory have been collecting long-term malaise trap data dating back to 1984. This has captured trends in insect populations in Gothic, showing significant change in insects with climate change (Dalton et al. 2023). However, this study sampled from only one site, and so cannot capture how insect populations may differ with spatial variation. In this study, we sampled from three sites in the Gothic area spanning an elevational gradient of 2800 to 3350 meters. Insects were sampled at each site on 7-10 day intervals throughout the summers of 2025 and 2026. These samples were then identified to order and weighed to determine biomass.

Insect order biomass and abundance, and climatic variables were used to construct GLMMs which used predictors found significant in the Dalton et al. 2023 paper. Site, or elevation, and taxon described little variation in insect abundance and biomass. Models showed biomass and abundance to increase as days since snowmelt increase. However, using AIC tests to compare models for current year's and previous year's precipitations' correlation with biomass and abundance, I found that biomass increases with previous year's precipitation whereas abundance increases with the current year's precipitation. When comparing biomass and sampling day from 2025 and 2026 with biomass predicted from the last 20 years' average of snowmelt time, the model suggested an earlier insect phenology relative to historic trends.

Introduction

Insects are an often overlooked yet crucial component of ecosystems (Schowalter et al. 2018). Declines in invertebrate populations affect decomposition, insectivore fitness, pollination, and agriculture (Wagner et al. 2021)— consequences which will only continue to snowball as 40% of insect species are threatened with extinction worldwide (Sánchez-Bayo et al. 2019). Despite their ecological importance and what some call the "insect apocalypse" (Goulson 2019), more charismatic or economically significant species remain the focus of research (Troudet et al. 2017), leaving a taxonomic gap for invertebrates.

Factors negatively influencing insect populations include habitat loss, pollution and insecticides, and introduced species (Scherber et al. 2026). However, even in remote ecosystems, insect abundances have shown declines as dramatic as ~61.5% from 1986 to 2020 in a North American sub-alpine community (Dalton et al., 2023). This phenomenon coincides with the impacts of climate change in the ecosystem, which have been shown to influence the phenology of host plants, precipitation, snowmelt time, and warming temperatures at the same site (Inouye 2020).

An understanding of how insect communities respond to changing environmental conditions across a spatial gradient can aid in predicting how their abundances, biomass, and emergence times may shift as a consequence of the changing climate in high-elevation ecosystems. The same environmental changes may affect high elevation insect assemblages differently compared to lower elevation assemblages, even if their compositions are similar. Members of the same species can have different traits selected for in each environment, so may respond differentially to the same pressure (Damasceno et al. 2026). Understanding spatial variation in insect response to phenological shifts would not only inform the conservation of insects but also the many species which rely on them such as insectivores and mutualists.

Previous work has shown that insect abundance is influenced by the timing of snowmelt, temperature, and previous year's precipitation (Uphus et al. 2023), though this has yet to be tested across a spatial gradient at RMBL. Therefore, this study explores how insect communities across a spatial gradient respond to environmental factors. I hypothesized that insect communities are shifting their phenology in response to a changing climate, but that these phenological shifts vary with elevation and by insect order. I expected to see that between insect orders, we would see different responses to climatic variables. I also predicted that the overall shift for all elevational communities would be advanced earlier in the year compared to historical insect communities because of the earlier snowmelt at all sites resulting in an earlier spring for insects to exploit.

Methods

We collected malaise trap data at three sites surrounding the Rocky Mountain Biological Laboratory (RMBL) in the montane meadow habitats around Gothic, Colorado between May and August of 2026. Sites include lowland wet meadow/willow thicket sites throughout East River Valley, Schofield Park, and North Pole established by Dr. Savannah Troy spanning 2867-3350m of elevation.

The new sites were sampled using the same methods described by Dalton et al. 2023, extending the historical data set. We collected insects by opening malaise traps for 48 hours per week with 95% ethanol kill jars. We then identified the insect specimens to order and recorded the abundance of each order. After 72 hours of drying, we weighed the biomass of diptera, hymenoptera, and combined other orders (lepidoptera, coleoptera, hemiptera, leafhoppers, and grasshoppers, mainly). To monitor environmental conditions at each site, we recorded rainfall in a passive rain gauge in 2026 and sourced precipitation data from daymet for 2025 (Thornton et al. 2022). I used rainfall data from daymet to sum the precipitation from the time between samples, giving summed precipitation for 2025. Our rain gauges collected rainwater all week and were checked and emptied when samples were collected, giving summed weekly rainfall for 2026. Temperature data on the mean temperature for the week was also derived from daymet and the date of bare ground was sourced from the RMBL Spatial Database (Breckheimer 2022). Statistical analyses were modeled off of select analyses from the Dalton et al. 2023 paper, however, the model was adjusted to also account for spatial variance and elevation, lending an understanding of how these communities may differ.

I constructed generalized linear mixed effect models (GLMMs) using the glmmTMB package in R to test which predictors were significant for insect abundance and biomass. Models showed precipitation and temperature to be highly correlated with an R value of -0.474401, too high to include both predictors in the same model. So, precipitation was ultimately used because temperature data was not yet available for 2026.

These GLMMs were constructed to evaluate predictors of insect biomass and abundance with AIC. The model formulations for biomass, where predicted insect biomass is *wt*, were:

$logit(wt) = a + \beta_1$ *previous year's precipitation* $+ \beta_2$ *days since snowmelt* $+ \beta_3$ *snow squared* $+ \beta_4$ *year + order + site*

(Model 1.1)

$logit(wt) = a + \beta_1$ *current year's precipitation* $+ \beta_2$ *days since snowmelt* $+ \beta_3$ *snow squared* $+ \beta_4$ *year + order + site*

(Model 1.2)

The model formulations for abundance, where predicted insect abundance is *n*, were:

$logit(n) = a + \beta_1$ *current year's precipitation* $+ \beta_2$ *days since snowmelt* $+ \beta_3$ *snow squared* $+ \beta_4$ *year + order + site*

(Model 2.1)

$logit(n) = a + \beta_1$ *previous year's precipitation* $+ \beta_2$ *days since snowmelt* $+ \beta_3$ *snow squared* $+ \beta_4$ *year + order + site*

(Model 2.2)

In both models, $\beta_{1\text{-}4}$ indicate fixed effects. Current year's precipitation measures weekly total and previous year's precipitation measures annual cumulative precipitation (mm) during sampling weeks, and days since snowmelt is calculated with the date the malaise trap was opened minus the date of snowmelt for that year. Precipitation and days since snowmelt were scaled in these models to make effect size comparable. Snow squared is the date of snowmelt variable squared to demonstrate the quadratic relationship of insect biomass and abundance with snowmelt. "Order" is a random effect term for taxonomic order identified in each sample. "Site" is a random effect based on each location of our malaise traps, which fall along an elevational gradient. These predictors in the model were selected based on what was found significant in the Dalton et al. 2023 paper and what climate data was available for analysis this year. All numerical predictors were centered and scaled prior to analysis.

Additionally, the mean date of snowmelt from 1993 to 2022 from the RMBL Spatial Database was used to predict what insect biomass would have looked like in a year when snowmelt happened later in the year, as it was historically. I tested both quadratic and linear models of biomass and date of snowmelt with AIC model comparison. With this, I compared the relationship between biomass and sampling date in 2025, 2026, and historically.

All analyses were done in RStudio v. 4.5.2 (Posit Team 2025) using packages terra (Hijmans et al. 2026), sf (Pebesma et al. 2023), daymetr (Hufkens et al. 2018), and tidyverse (Wickham et al. 2019) for spatial data and climate variables at sampling sites, and using the package glmmTMB (Brooks et al. 2017) for modelling. I determined statistical significance to be p-values less than 0.05, and included 95% confidence intervals in plots.

Results

Based on AIC scores, I found that biomass was better predicted by the previous year's precipitation ($p = 0.000733$) whereas abundance was better predicted by the current year's precipitation ($p = 2.12e-06$); however, both periods of precipitation were significant (Table 1). Models 1.1 and 2.1 indicated that in years with higher weekly cumulative precipitation, insect abundance was higher and with increased cumulative precipitation in the previous year, biomass was also higher (Tables 2 and 3).

AIC scores evaluating biomass' relationship with date of snowmelt demonstrated that the quadratic model (AIC = -65.282) was a better fit than linear model (AIC = -49.138). Both biomass and abundance models showed a positive relationship with days since snowmelt, indicating that as the date gets further from snowmelt, insect biomass and abundance increases (Tables 2 and 3). Contrary to my predictions, I found that very little variance in insect biomass and abundance was described by order (variance described = 4.96e-02 ± 2.23e-01) or site (variance described = 3.94e-10 ± 1.98e-05) (Table 4).

The predicted insect biomass based on historical snowmelt date indicated a slight advancement in phenology for 2025 and 2026 compared to the historical average, but the 95% confidence intervals for all 3 groups overlap indicating that this difference is not significant (Figure 3).

Discussion

Site and taxon's explanation of little variance (Table 4) indicates that across elevations and invertebrate orders, the within-season changes in abundance and biomass were very similar. For taxon, orders being clumped together rather than identified and modeled at a species-specific level may explain why there was no taxonomic difference. Identification of the malaise trap samples to greater specificity – e.g., to family or genus– could lead to some taxonomic significance being demonstrated. The site's lack of significance to insect biomass and order indicates that the spatially distinct communities were not significantly different despite the 550 meter elevational gradient. This may be because snowmelt has advanced so much earlier at high sites due to climate change that the community is no longer significantly different from our low elevation site that already had an early snowmelt time. An earlier snowmelt at high elevations could mean less water availability in the late summer, stressing the ecosystem (Gillian et al. 2010). In effect, we could see decreased insect abundance at the end of summer compared to years with a later snowmelt. Earlier melting and decreased snowpack in the winter also means that overwintering insects have less protection from the cold weather, reducing the survivability of these species (Ziadeh et al. 2024).

Biomass and abundance's differing predictors of year of precipitation may indicate a species-specific relationship to rainfall. It may be that insects with a life cycle that relies on the current year's rainfall are particularly abundant but lightweight (Valdez et al. 2017), or that heavier insects happen to have life cycles relying on the previous year's precipitation (Prinster et al. 2020). Figure 1 also shows diptera with significantly higher abundance than hymenoptera and other orders, whereas biomass orders overlap completely. Malaise traps are biased towards flighted insects including diptera and hymenoptera (Haas 2026), indicating that this ecosystem is more abundant in diptera than hymenoptera in this part of the summer. However, it does not fully represent the abundance of other orders that are not sampled representatively by malaise traps.

Figures 2 and 3 demonstrate an increase in both insect abundance and biomass as the year progresses rather than a quadratic relationship we might expect as insect populations increase at the start of summer and decrease at the end. This is likely because the 2025 and 2026 insect data sets did not capture the decrease in insects at the end of the summer. This quadratic relationship may be demonstrated after the last malaise trap samples from 2026 are processed and added to the data set. Despite this, we still see the expected trend of increasing numbers and weight of bugs at the beginning of the summer in Figures 2 and 3. Figure 3, however, shows the trend lines for 2025 and 2026 to be shifted left of the historical line, although their 95% confidence intervals overlap, so they are not significantly different at this point. Still, it suggests an advanced phenology in 2025 and 2026 compared to historical values, indicating that insects in current years may be emerging and experiencing their peak earlier than they did historically because of the earlier snowmelt time. As ecosystems rely on insects in many ways, as prey for insectivores, as pollinators, and as detrivores, this phenological shift could have ecological consequences if mismatches with other species are large enough in magnitude and direction. Relationships of insects with host plants shift with environmental change if symbiotic species respond differently with germinating time and development to the same environmental cues (Gérard et al. 2020). Similarly, insectivores and insects can misalign, leading to uncontrolled insect populations and increased herbivory by insects, a trophic cascade resulting in a decline in plant biodiversity, soil quality (Fang et al. 2026), and possibly decreased insectivore fitness.

If these malaise traps across an elevational gradient accrue data over more years, a trend in how spatially different insect communities respond to the changing environment differently may be revealed. Further identification of the insect specimens to family or order could reveal more specific relationships with climatic variables like precipitation. A completed 2026 data set showing the decline in insects at the end of the season may also show differences from historical insect communities. It is possible that insects are exploiting a longer season than they used to, or they may be declining earlier due to decreased water availability at the end of summer.

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Tables and Figures

Table 1:
GLMMs for insect abundance and biomass predicted by current and previous year's precipitation evaluated with an AIC model comparison test.

	Current Year's Precipitation AIC	**Previous Year's Precipitation AIC**
Insect biomass (g)	-160.020 (Model 1.2)	-163.398 (Model 1.1)
Insect abundance	3253.746 (Model 2.1)	3275.854 (Model 2.2)

Table 2: Insect biomass (Model 1.1)
GLMM coefficient estimates predicting insect biomass using precipitation of the previous year.

	P-value	**Estimate**
Days since snowmelt	0.000257	0.449 ± 0.256

Cumulative Precipitation of Previous Year	0.000733	0.608 ± 0.180
Year of 2026 (2025 is reference)	0.000919	1.17 ± 0.354

Table 3: Insect abundance (Model 2.1)
GLMM coefficient estimates predicting insect abundance using precipitation of the current year.

	P-value	**Estimate**
Days since snowmelt	< 2e-16	0.261 ± 0.0139
Cumulative Precipitation of Current Year	2.12e-06	0.0567 ± 0.0120
Year of 2026 (2025 is reference)	<2e-16	-0.449 ± 0.0262

Table 4: Variance in insect biomass and abundance described by random effects of taxon and site.

	Variance Described in Biomass (Model 1.1)	**Variance Described in Abundance (Model 2.1)**
Taxon	4.96e-02 ± 2.23e-01	0.233 ± 0.483
Site	3.94e-10 ± 1.98e-05	0.00744 ± 0.0863

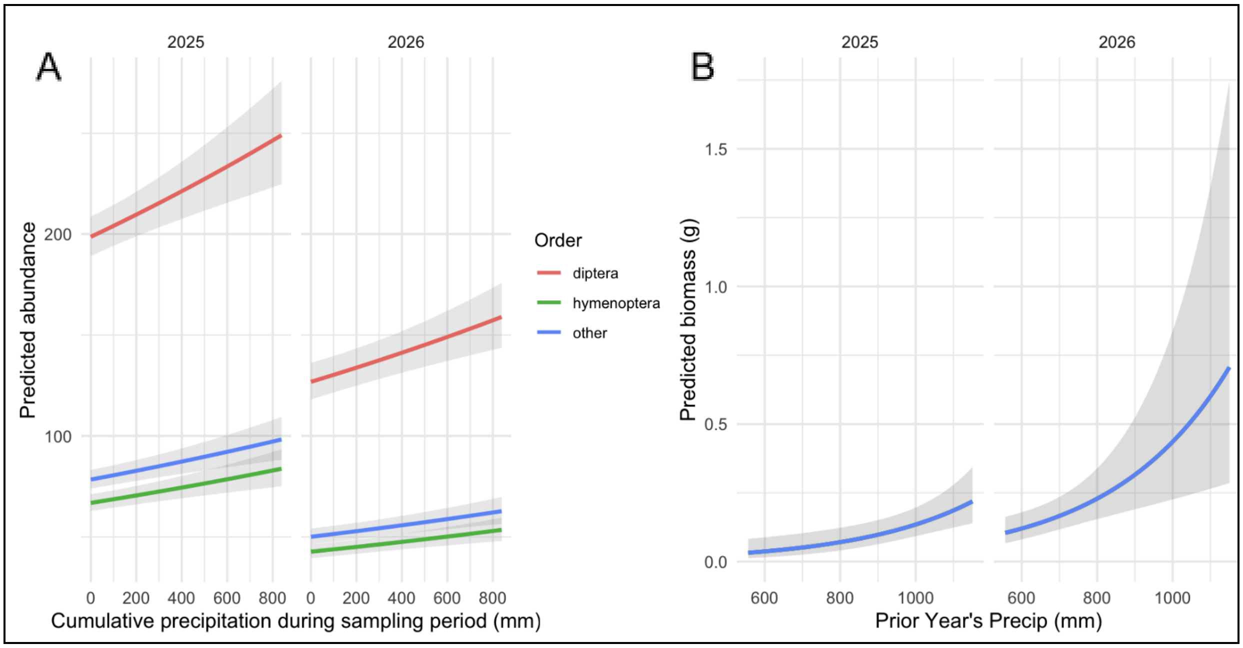

Figure 1. A) Marginal effect of cumulative precipitation of current year (mm) on predicted abundance response in a generalized linear mixed model. (Model 2.1) Invertebrate abundance increases with weekly cumulative precipitation, with diptera having significantly higher abundance than other orders in both 2025 and 2026. B) Marginal effect of cumulative precipitation of previous year (mm) on predicted biomass (g) response in a generalized linear mixed model. (Model 1.1) Invertebrate biomass increases with weekly cumulative precipitation in both 2025 and 2026.
Grey ribbon in both plots demonstrates a 95% confidence interval.

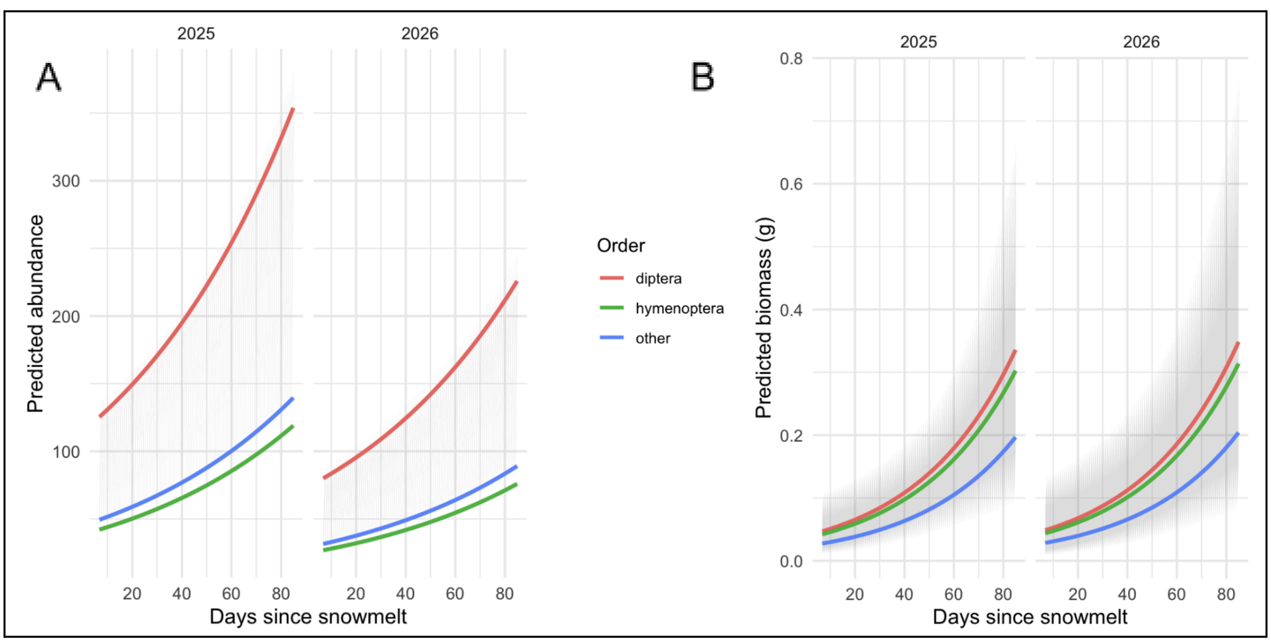

Figure 2. Marginal effect of days since snowmelt on predicted abundance (A) and biomass (B) responses in a generalized linear mixed model. A) Invertebrate abundance increases as days get further from the day of snowmelt in both 2025 and 2026. B) Invertebrate biomass increases as days get further from the day of snowmelt in both 2025 and 2026. Grey ribbon in both plots demonstrates a 95% confidence interval.

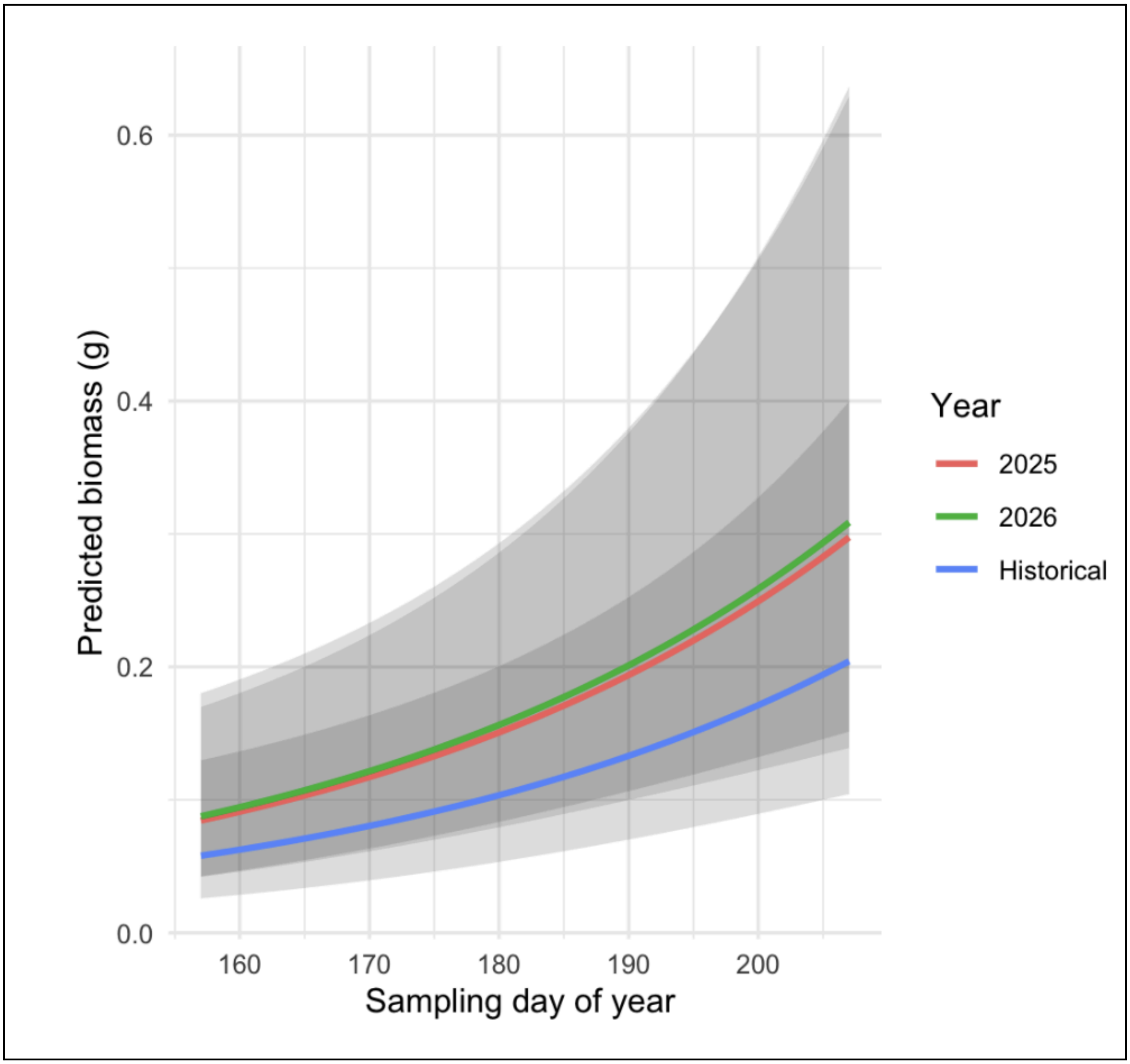

Figure 3. Marginal effect of sampling date on predicted invertebrate biomass response in a generalized linear mixed effect model. Years 2025, 2026, and historical lines are plotted, using the mean date of bare ground from the past 20 years as a historical biomass predictor. Grey ribbon demonstrates a 95% confidence interval.