Climatic Unpredictability and Parasitism of Caterpillars: Implications of Global Warming

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Available at: https://works.bepress.com/robert-marquis/29/
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Insect outbreaks are expected to increase in frequency and intensity with projected changes in global climate through direct effects of climate change on insect populations and through disruption of community interactions. Although there is much concern about changes in global climate, the impact of climatic variability itself on species interactions has been little explored. Here, we compare caterpillar–parasitoid interactions across a broad gradient of climatic variability and find that the combined data in 15 geographically dispersed databases show a decrease in levels of parasitism as climatic variability increases. The dominant contribution to this pattern by relatively specialized parasitoid wasps suggests that climatic variability impairs the ability of parasitoids to track host populations. Given the important role of parasitoids in regulating insect herbivore populations in natural and managed systems, we predict an increase in the frequency and intensity of herbivore outbreaks through a disruption of enemy–herbivore dynamics as climates become more variable.

Materials and Methods

We summarized overall parasitism data from 15 Lepidoptera rearing programs from a broad spectrum of climatic regimes and locations from the region between southern Canada and central Brazil (Table 1). These inventories focused on Macrolepidoptera, which largely feed externally on leaves, but we have included data for non-leaf-mining Microlepidoptera as well. Data from these inventories range from 616 to 130,000 individual records of laboratory rearings of wild-caught caterpillars comprising 40 to thousands of species of Lepidoptera in each case (Table 1). When a study is ongoing, records only up through 2003 were used. Each of these studies involved collecting caterpillars from the field and rearing them on their host plants in plastic bags or other sealed containers until pupation or emergence of parasitoids. Other than the ACG, Maryland, and Brazil inventories (which rear all instars encountered), inventories tended to focus collections on later (penultimate/ultimate) instar caterpillars to maximize opportunities for parasitism in the field. From these data, we obtained the total proportion of collected caterpillars that were parasitized by parasitoid wasps (Hymenoptera) and tachinid flies (Tachinidae) among all host species. In all cases, observed parasitism frequencies are likely to represent underestimates because collecting individuals...
from the field for rearing largely removes them from further risk of parasitism. For each of the caterpillar inventories, we determined the latitude and calculated the coefficient of variation (CV) in year-to-year precipitation with data sets ranging from 12 to 144 years. For studies conducted in areas without on-site weather stations, we acquired weather data from the closest sampling stations. Estimates of parasitism frequency were arcsine transformed for statistical analysis (but not for display in Figs. 1 and 2). Simple linear least-squares regressions (weighted by sample size) were calculated to estimate the effects of climatic variability on frequency of parasitism. One-tailed tests of significance were formed for statistical analysis (but not for display in Figs. 1 and 2).

Results and Discussion

A regression of frequency of overall parasitism of caterpillars from each of the inventory rearing programs against local yearly variation in amount of precipitation (expressed as the CV) reveals a significant relationship in the predicted direction: overall parasitism frequency decreases as climatic variability increases ($R^2 = 0.37, F_{1,14} = 7.69, P = 0.016$; Fig. 1). Although an overall frequency of parasitism is a complex community variable that is influenced by many interacting factors and levels of parasitism have high variances within any given forest, the strong relationship with precipitation suggests that it is reasonable to assign a characteristic level of parasitism to an ecosystem in a particular place. The relationship in Fig. 1 explains over one-third of the total variation in caterpillar parasitism despite a wide diversity of host and parasitoid species and a broad diversity of ecosystems at different latitudes. The exceptionally low parasitism (7%) from the wet forest of the ACG is perhaps due to the fragmented nature of this site and the inclusion of copious data from larvae collected in their early instars. When this single outlier is excluded, the relationship between climatic variability and precipitation is even stronger ($R^2 = 0.59, F_{1,13} = 17.16, P = 0.0014$).

Reduced frequency of parasitism with increasing climatic variability is unrelated to tropical–temperate disparities in parasitism because latitude (arc sine transformed) exerted no significant effect either independently ($R^2 = 0.013, F_{1,14} = 0.17, P = 0.69$) or in a multiple regression with precipitation variability ($R^2 = 0.018, F_{1,14} = 0.69$).
between parasitism and climatic variability ($R^2 = 0.68, F_{1,9} = 19.4, P = 0.002$; Fig. 2). Furthermore, the lack of a significant correlation between tachinid parasitism and climatic variability shows that an increase in tachinid parasitism does not occur as a reaction to the decrease in parasitism by Hymenoptera in more variable climates (i.e., their ecological roles are not interchangeable).

Further evidence that asynchronies between herbivore and enemy populations contribute to outbreak dynamics comes from the dramatic climatic fluctuations associated with El Niño events. These climatic fluctuations appear to be responsible for increases in herbivore population sizes through disruption of enemy–herbivore interactions (15). Temporal mismatches in parasitoid–host activity have also been suggested for extra-tropical latitudes; climate change can, for example, decouple populations of the economically important spruce budworm from populations of important enemy species such as invertebrate predators and birds (25). Short-term seasonal “boom-bust” dynamics of caterpillar populations have also been attributed to interactions between herbivores and their parasitoids and predators (26), suggesting that increases in seasonality may initiate or decelerate these cycles.

An extrapolation from the cross-geography relationship between climatic variability and parasitism demonstrated here, to temporal patterns in climate that may be associated with global warming, suggests that the frequency and perhaps intensity of herbivore outbreaks will likely increase with increased global warming. Given the potentially large economic and environmental impacts of herbivore outbreaks (7), these indirect effects of climate change via disruption of enemy–herbivore dynamics could be as disruptive as some of the more direct effects of global warming. Increased frequency or severity of herbivore outbreaks may add to the direct effects of global warming and climate change on plants. The indirect effects of climatic unpredictability on herbivores through disruption of enemy–pest relationships may be most visible in agricultural systems. For example, many species of parasitic wasps have been and continue to be used in biological control programs, often with appreciable success (27). Increases in climatic unpredictability could compromise their ability to control important crop pests, leading to increased use of pesticides.

Although the pattern we disclose provides a mechanism to explain associations between outbreaks of forest pests and climate change (3), it is difficult to make specific predictions as to how climates will change and how these changes will impact specific herbivore–parasitoid associations. Long-term monitoring of the demographics of herbivores and their associated parasitoids in response to climate, as well as more geographically detailed models of local climate change, will be necessary to predict the responses of ecological communities. We predict that the results of such detailed monitoring are likely to provide additional incentives to slow anthropogenic contributions to global climate change.

We thank a large number of parataxonomists at all sites for excellent field assistance and more than 150 taxonomists for their pro bono identifications underpinning these inventory projects. Financial support was provided by multiple grants from the National Science Foundation’s Division of Environmental Biology, the Department of Energy’s National Institute for Global Environmental Change, the Earthwatch Institute, the Missouri Department of Conservation, the Smithsonian Tropical Research Institute, and the respective institutional field stations where the inventories were carried out.

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