Climatic unpredictability and parasitism of caterpillars: Implications of global warming

J. O. Stireman III*†, L. A. Dyer*‡, D. H. Janzen‡§, M. S. Singer¶, J. T. Lill‖**, R. J. Marquis**, R. E. Ricklefs**, G. L. Gentry*, W. Hallwachs§, P. D. Coley††, J. A. Barone††, H. F. Greeney‡‡, H. Connahs*‡‡, P. Barbosa§§, H. C. Morais¶¶, and I. R. Diniz¶¶

*Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118; §Department of Biology, University of Pennsylvania, Philadelphia, PA 19104; ¶Department of Biology, Wesleyan University, Middletown, CT 06459; ‖Department of Biological Sciences, George Washington University, Washington, DC 20052; **Department of Biology, University of Missouri, St. Louis, MO 63121; ††Department of Biology, University of Utah, Salt Lake City, UT 84112; ‡‡Yanayacu Biological Station and Center for Creative Studies, Cosanga, Napo, Ecuador c/o Foch 721 y Juan Leon Mera, Quito, Ecuador; §§Department of Entomology, University of Maryland, College Park, MD 20742; and ¶¶Department of Ecology/Zoology, University of Brasilia, 70910-900, Brasilia, Brazil

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 mean 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.

climate change | herbivore | outbreak | parasitoid | top-down

Understanding the effects of rapid climate change on ecosystems and species is an important goal of modern ecological research. Several studies have documented recent vertebrate, invertebrate, and plant range shifts that are associated with global warming (1, 2). Additional studies have demonstrated changes in ecological interactions and potential changes in ecosystem function that are associated with climate change (3, 4). Increased unpredictability and variability in regional climates, particularly with regard to precipitation, should be exceptionally disruptive: models of climate change have predicted greater frequency and duration of droughts in some areas (5, 6), increased periods of high precipitation in others (6, 7), and a widespread increase in the frequency of extreme weather events (8, 9). Relatively few studies have addressed the potential effects of increased variation in precipitation or temperature on the relationships within biotic communities (10, 11), but given the strong dependence of many organisms on particular climatic signals and precipitation levels, it is likely that such effects will be profound.

Recent studies of forest insects have linked population outbreaks to phenological changes in insect life histories brought about by global climate change (12–15). Such analyses have predicted increased frequencies of outbreaks (13, 16) and longer durations of outbreaks (17). These studies have focused on the direct effects of climate change on herbivore life histories and subsequent population dynamics. However, the influence of climate change on higher trophic levels (e.g., predators and parasitoids) and the indirect effect that this may have on herbivores have not been considered. Herbivores can often respond rapidly and dramatically to changes in climatic conditions that influence development (e.g., timing of precipitation and dates of seasonal temperature change), leading to large temporal variance in herbivore populations. Parasitoids and other enemies may be affected by both the unpredictable climatic variation itself and the unpredictable amplified variance in host dynamics in response to climate. The inevitable lags associated with this additional variability may reduce the ability of parasitoids to track host or prey populations, resulting in a reduced average frequency of parasitism or reduced parasitism at key points in the cycle of herbivore–carnivore interactions. Documenting such processes is difficult. However, comparison of parasitism frequencies of caterpillars across geographic localities that differ in their climatic predictability provides a view of the potential effects of projected increases in climatic variability over time. Several recent intensive rearing programs of caterpillars collected from natural ecosystems have recorded frequency of parasitism (e.g., ref. 18; http://janzen.sas.upenn.edu; www.caterpillars.org; and Table 1). Here, we employ data from 15 of these inventories to relate parasitism frequency to climatic variability and discuss the mechanisms potentially responsible for the emergent pattern.

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

Table 1. Caterpillar rearing databases used in the current study

Study location	Code	Country	Latitude	Ave. precipitation ± SD (years)	Rearings	Species	Years	Ref.
Southeast Arizona	AZ	United States	31°43′N	30.5 ± 8.7 (30)	9,000	167	6	19
Area de Conservación Guanacaste (dry forest)	ACGd	Costa Rica	10°50′N	162.2 ± 46.2 (51)	121,430	>1,000	27+	18
Area de Conservación Guanacaste (wet forest)	ACGw	Costa Rica	10°50′N	283.0 ± 58.1 (12)	44,725	>400	10+	18
La Selva Biological Station	LS	Costa Rica	10°25′N	423 ± 69.6 (44)	50,000	>700	10	20
Yanayacu Biological Station	YBS	Ecuador	0°25′S	452.8 ± 52.9 (16)	10,000	>200	2	H.F.G., et al., unpublished work
Southeast Louisiana	NO	United States	29°50′N	161.2 ± 35.7 (35)	1,574	44	2+	J.O.S., L.A.D., and G.L.G., unpublished work
Reserva Ecológica do IBGE	Bra	Brazil	15°56′S	144.9 ± 16.7 (23)	8,091	450	10+	28
Barro Colorado Island (STRI)	BCI	Panama	9°10′N	263.3 ± 46.1 (74)	1,267	>100	3	P.D.C. and J.A.B., unpublished work
Parque Nacional Metropolitana	PNM	Panama	8°55′N	177.8 ± 26.84 (72)	805	69	1	L.A.D. and H.C., unpublished work
Fort Sherman	FS	Panama	9°16′N	323.9 ± 49.8 (28)	616	62	1	L.A.D. and H.C., unpublished work
Southern Ontario	Can	Canada	45°45′N	81.3 ± 11.7 (144)	78,337	43	10	29
Connecticut	CN	United States	41°24′N	112.9 ± 19.5 (49)	844	55	1	M.S.S., unpublished work
Maryland	MD	United States	39°15′N	108.6 ± 19.8 (102)	3,699	82	5	30
Southern Missouri	MO	United States	37°1′N	113.8 ± 26.6 (56)	3,104	100+	3	31
Virginia/West Virginia	VA	United States	37°55′N	97.9 ± 16.7 (98)	5,235	46	2	32

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 station with similar climate from the Global Precipitation Climatology Centre (19). For La Selva Biological Station (Costa Rica), the Reserva Ecológica do IBGE (Brazil), and the Smithsonian Tropical Research Station on Barro Colorado Island (Panama), we acquired records taken directly from the field 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 used in analysis evaluating our hypothesis that parasitism levels decrease with increased climatic unpredictability. For four data sets (MO, PNM, FS, and BCI), we were unable to obtain reliable estimates of the proportion of parasitism due to parasitic wasps versus tachinid flies, and thus these data were not included in specific analyses focusing on these taxa.

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 (arcsine 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 ($R^2 = 0.018$, $F_{1,14}$
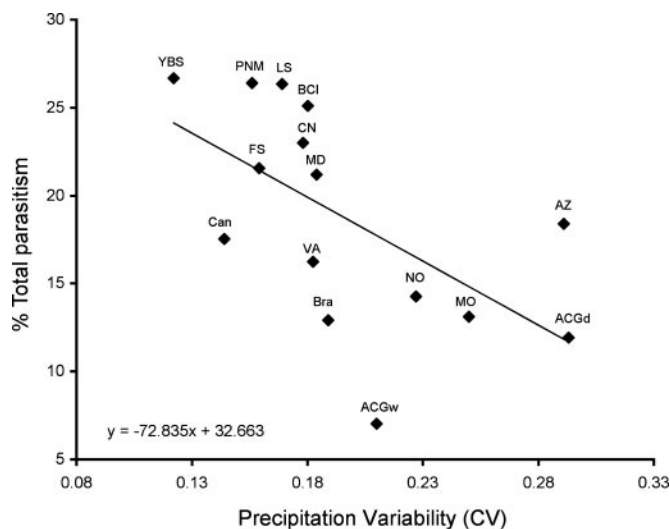

Fig. 1. A linear regression of total parasitism levels of caterpillars from 15 extensive rearing programs against year-to-year variability in precipitation (CV; $R^2 = 0.37$). Letter codes correspond to sites of rearing studies (Table 1).

Fig. 2. A linear regression of larval parasitism by only parasitoid wasps against year-to-year variability in precipitation (CV; $R^2 = 0.68$). Data sets that did not identify parasitoids were not included in the regression.

$= 0.26$, $P = 0.62$). Likewise, previous work has shown that no large-scale relationships exist between parasitism frequency and mean temperature or annual range in temperature across ecosystems and latitudes (20). Average precipitation among sites also fails to explain significant variation in parasitism frequency ($R^2 = 0.18$, $F_{1,14} = 2.78$, $P = 0.12$). We hypothesize that the negative association between parasitism frequency and climatic variability displayed in Fig. 1 is the result of increased lags and disconnections between herbivores and their carnivores that occurs as climatic variability increases. Because parasitism frequencies of herbivores are strongly correlated with the degree of population regulation by parasitoids (21), understanding the underlying mechanism for the negative association may help predict the frequency of future insect outbreaks in tropical and temperate ecosystems as climate change accelerates [as it is predicted to do by some models (22)].

If the observed relationship between precipitation variability and parasitism results from a decrease in the ability of a parasitoid population to survive on a caterpillar population of a given density, then it follows that highly host-specific parasitoids will suffer disproportionately as populations fluctuate (23). Host-specific parasitoids should be more sensitive than generalists to variation in host emergence time or developmental rate. Out-of-phase specialist parasitoids may miss narrow windows of host vulnerability of their particular hosts. In contrast, because generalists exploit a variety of hosts that might individually respond to climatic cues in different ways, they should be less susceptible to the host population lags and asynchronies associated with climatic unpredictability. This prediction is supported by the contrasting ways that the two major groups of parasitoids correlate with climatic variability in our analysis. Many species of tachinid flies possess relatively large host ranges (http://janzen.sas.upenn.edu; www.caterpillars.org; ref. 24), and frequency of parasitism by tachinids exhibits no relationship with climatic variability among the data sets that estimated their frequency ($R^2 = 0.009$, $F_{1,9} = 0.08$, $P = 0.78$). Parasitism by parasitoid wasps that are on average relatively host-specific (http://janzen.sas.upenn.edu; ref. 20), however, correlates strongly with climate variability, driving the entire relationship

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 extratropical latitudes; climate change can, for example, decouple populations of the economically important spruce budworm from populations of important enemies 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 exacerbate 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.

1. Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., *et al.* (1999) *Nature* **399,** 579–583.
2. Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M. & Conradt, L. (2001) *Nature* **411,** 577–581.
3. Harrington, R., Woiwod, I. & Sparks, T. (1999) *Trends Ecol. Evol.* **14,** 146–149.
4. Pounds, J. A. & Puschendorf, R. (2004) *Nature* **427,** 107–109.
5. Hulme, M. & Viner, D. (1998) *Clim. Change* **39,** 145–177.
6. Dai, A., Trenberth, K. E. & Karl, T. R. (1998) *Geophys. Res. Lett.* **25,** 3367–3370.

7. Groisman, P. Y., Karl, T. Y., Easterling, D. R., Knight, R. W., Jamason, P., Hennessy, K. J., Suppiah, R., Page, C. M., Wibig, J., Fortuniak, K., *et al.* (1999) *Clim. Change* **42,** 243–283.
8. Kunkel, K. E., Pielke, R. A. & Changnon, S. A. (1999) *Bull. Am. Meteorol. Soc.* **80,** 1077–1098.
9. Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R. & Mearns, L. O. (2000) *Science* **289,** 2068–2074.
10. Coley, P. D. (1998) *Clim. Change* **39,** 315–328.
11. Parmesan, C., Root, T. L. & Willig, M. R. (2000) *Bull. Am. Meteorol. Soc.* **81,** 443–450.
12. Ayres, M. P. & Lombardero, M. J. (2000) *Sci. Total Environ.* **262,** 263–286.
13. Williams, D. W. & Liebhold, A. M. (1995) *Environ. Entomol.* **24,** 1–8.
14. Volney, W. J. A. & Fleming, R. A. (2000) *Agric. Ecosyst. Environ.* **82,** 283–294.
15. Hodar, J. A. & Zamora, R. (2004) *Biodiversity Conserv.* **13,** 493–500.
16. Fleming, R. A. & Volney, W. J. A. (1995) *Water Air Soil Pollut.* **82,** 445–454.
17. Logan, J. A., Regniere, J. & Powell, J. A. (2003) *Front. Ecol. Environ.* **1,** 130–137.
18. Stireman, J. O., III, & Singer, M. S. (2003) *Ecology* **84,** 296–310.
19. Rudolf, B., Hauschild, H., Rueth, W. & Schneider, U. (2002) in *Global Precipitation and Climate Change*, eds. Desbois, M. & Desalmond, F. (Springer, New York), NATO ASI Series I, Vol. 26, pp. 173–186.
20. Hawkins, B. A. (1994) *Pattern and Process in Host–Parasitoid Interactions* (Cambridge Univ. Press, New York).
21. Hawkins, B. A. & Cornell, H. V. (1994) *Science* **266,** 1886.
22. National Assessment Synthesis Team (2001) *Climate Change Impacts on the United States: The Potential Consequences of Climate Variability and Change, Report for the U.S. Global Change Research Program* (Cambridge Univ. Press, Cambridge, U.K.).
23. Janzen, D. H. (1981) *Ecology* **62,** 532–537.
24. Belshaw, R. (1994) in *Parasitoid Community Ecology*, eds. Hawkins, B. A. & Sheehan, W. (Oxford Univ. Press, Oxford), pp. 145–162.
25. Mattson, W. J. & Haack, R. A. (1987) *Bioscience* **37,** 110–118.
26. Morais, H. C., Diniz, I. R. & Silva, D. M. S. (1999) *Rev. Biol. Trop.* **47,** 1025–1033.
27. Greathead, D. (1986) in *Insect Parasitoids, 13th Symposium of the Royal Entomological Society of London*, eds. Waage, J. & Greathead, D. (Academic, London), pp. 289–318.
28. Diniz, I. R. & Morais, H. C. (1997) *Biodiversity Conserv.* **6,** 817–836.
29. Lill, J. T., Marquis, R. J. & Ricklefs, R. E. (2002) *Nature* **417,** 170–173.
30. Barbosa, P., Segarra, A. E., Caldas, A., Gross, P., Ahlstrom, K., Carlson, R. W., Ferguson, D. C., Grissell, E. E., Woodley, N. E., Hodges, R. W., *et al.* (2001) *Ecology* **82,** 698–704.
31. Le Corff, J., Marquis, R. J. & Whitfield, J. B. (2000) *Environ. Entomol.* **29,** 181–194.
32. Petrice, T. R., Strazanac, J. S. & Butler, L. (2004) *J. Econ. Entomol.* **97,** 451–459.

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