

Notes and Comments

Transcontinental Crashes of Insect Populations?

Bradford A. Hawkins^{1,*} and Marcel Holyoak^{2,†}

1. Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697

2. Department of Entomology, University of California, Davis, California 95616-8584

Submitted December 4, 1997; Accepted March 17, 1998

Keywords: population dynamics, time series, drought, density-independent factors.

The sensitivity of insect populations to climate is universally appreciated (Andrewartha and Birch 1954; Lawton 1995). Climate can also synchronize populations of conspecifics over regional scales when dynamics are driven by similar density-dependent processes—the Moran effect (Moran 1953; Ranta et al. 1995, 1997; Royama 1996). However, the possibility that climatic events can also synchronize populations of many species over large geographic scales is less well documented.

During the late 1980s, the continental United States suffered a widespread drought, and several population biologists noted its impact on local insect population dynamics (Sumerford 1991; Price et al. 1995; Weiss 1996). These isolated, synchronized crashes led us to question the geographic scope of the drought and the responses to it by a wide range of insect species. To examine potential continental-scale effects, we compiled times series of abundances for North American insects encompassing the 1980s, with an effort to include as large a portion of North America as possible and a diverse set of insect taxa occupying a range of habitats. Our goal was to determine if the drought was widespread and severe enough to cause temporally synchronized population crashes across North America, independently of any density-dependent

factors that may be operating within the populations. Because our focus was on the drought, we also obtained records of annual precipitation for the regions where each insect population occurs for the period 1978–1996.

We located time-series data for 10 insect taxa, representing a wide range of life histories, habitats, and geographic regions in North America (references in fig. 1 legend): gypsy moth (*Lymantria dispar*, Lepidoptera: Lymantriidae) in Massachusetts; a multispecies complex of grasshoppers (Orthoptera: Acrididae) in Montana; pear psylla (*Cacopsylla pyricola*, Homoptera: Psyllidae) in Washington; western tent caterpillar (*Malacosoma plumiviale*, Lepidoptera: Lasiocampidae) in British Columbia; larch casebearer (*Coleophora laricella*, Lepidoptera: Coleophoridae) in Oregon; a willow-galling sawfly (*Euura lasiolepis*, Hymenoptera: Tenthredinidae) in Arizona; an oak leaf miner (*Cameraria hamadryadella*, Lepidoptera: Gracillariidae) in Virginia; an aspen leaf miner (*Phyllonorycter tremuloidiella*, Lepidoptera: Gracillariidae) in Minnesota; goldenrod gall fly (*Eurosta solidaginis*, Diptera: Tephritidae) in Pennsylvania; and bay checkerspot butterfly (*Euphydryas editha bayensis*, Lepidoptera: Nymphalidae) in northern California.

Insect population sizes were estimated by the original workers using a range of methods and at various spatial scales. Species varied in both their average abundance and in the amount of temporal variation in abundance. To facilitate comparisons among the different measures we therefore standardized the annual estimates of \log_{10} insect numbers (or \log_{10} acres defoliated in the case of gypsy moth) to a mean of 0 and unit standard deviation. Data for the entire available times series were used, with three exceptions. For gypsy moth and grasshoppers, post-1964 data were used to better focus the temporal trends on the 1987–1988 drought event. For *C. laricella*, an exotic species that was the target of a successful biological control program beginning in the mid-1970s, post-1984 data were used, after densities had fallen by an order of magnitude due to the actions of the introduced parasitoids (Ryan 1997). Finally, when we had multiple time series for a taxon, we arbitrarily selected one. The patterns are therefore illustrative.

* To whom correspondence should be addressed; E-mail: bhawkins@uci.edu.

† E-mail: maholyoak@ucdavis.edu.

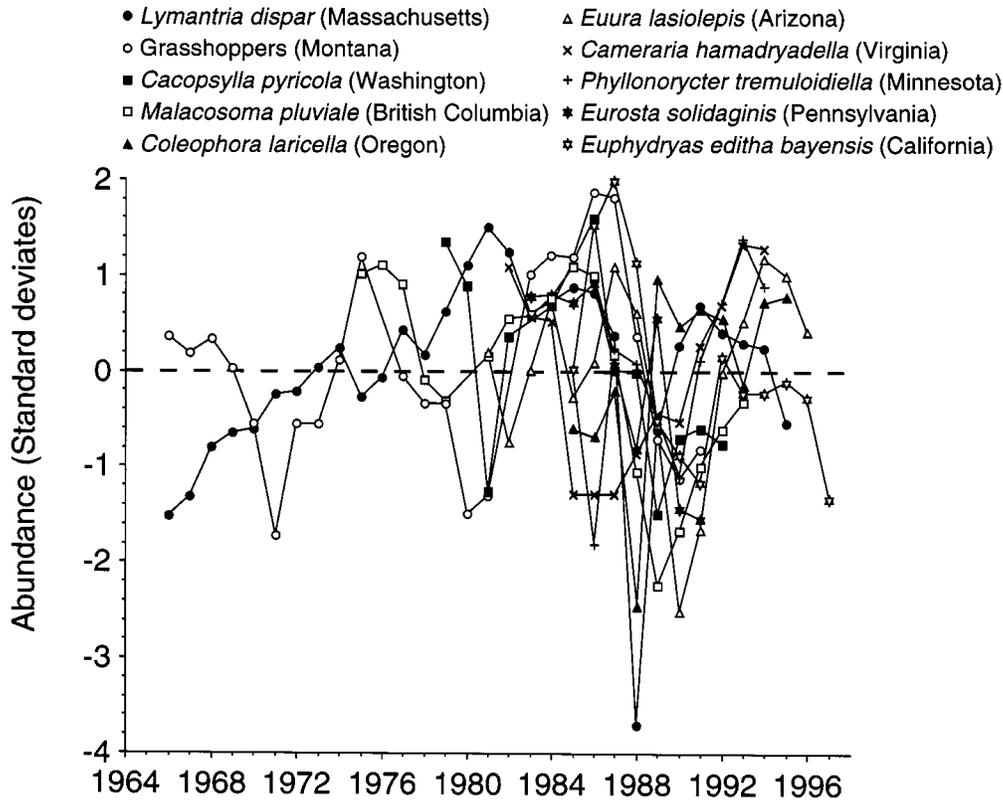


Figure 1: Temporal patterns of abundance for 10 North American insect taxa in standard deviations of \log_{10} abundance. The dashed horizontal line is mean abundance of each taxon standardized to 0. Data sources: *Lymantria dispar*—Massachusetts Department of Environmental Management (G. Dwyer, personal communication); grasshoppers—Kemp and Dennis (1993); *Cacopsylla pyricola*—Horton et al. (1992); *Malacosoma pluviale*—Myers and Rothman (1995); *Coleophora laricella*—Ryan (1990) and R. B. Ryan (personal communication); *Euura lasiolepis*—Price et al. (1995) and P. W. Price (personal communication); *Cameraria hamadryadella*—Auerbach et al. (1995) and M. J. Auerbach (personal communication); *Phyllonorycter tremuloidiella*—Auerbach et al. (1995) and E. F. Connor (personal communication); *Eurosta solidaginis*—Sumerford (1991) and D. V. Sumerford (personal communication); *Euphydryas editha bayensis*—Weiss (1996) and S. B. Weiss (personal communication).

The precipitation data were similarly transformed into standard deviates. We assume that insects are locally adapted to absolute rainfall levels and are most affected by deviations from average weather patterns.

The relationship between population levels and precipitation was tested by cross-correlation (Box and Jenkins 1976). The cross-correlation coefficient ($R_{xy(k)}$) represents the correlation between two series, x and y , where x is lagged by k observations. Cross-correlations examined the relationship between the proportions of sites with low rainfall and low insect abundances in each year (with “low” defined as less than 1 negative standard deviate), with potential lags of 0–5 yr. We conducted correlations between the proportion of sites with low abundances and low rainfall rather than between the average abundance and rainfall values in all years for each species because abundance may show responses to rainfall in nondrought years that could mask the correlation between low abundance and low rainfall.

Population trends during the 1980s indicate that, for a majority of species, populations were relatively high early in the decade, but all suffered population crashes between 1987 and 1990, rebounding in the early 1990s (fig. 1). This “cycle” was coincident with a relatively wet period in the early 1980s, followed by the drought in 1987–1988 (fig. 2). The cross-correlation analyses and plots of mean insect abundance and precipitation indicate depressed population levels across North America in response to the drought, both within the same year ($R_{xy(0)} = 0.531$, $t = 2.59$, $df = 17$, $P < .05$) and with a 1-yr lag ($R_{xy(1)} = 0.746$, $t = 4.62$, $df = 16$, $P < .01$; fig. 3). All other lags were nonsignificant ($P > .05$).

These data suggest that climatic extremes can synchronize insect population crashes at the continental scale. Further, unlike the Moran effect, in which climatic perturbations generate synchronization when populations share density-dependent regulatory factors, the crashes due to the drought affected species in a diverse range of

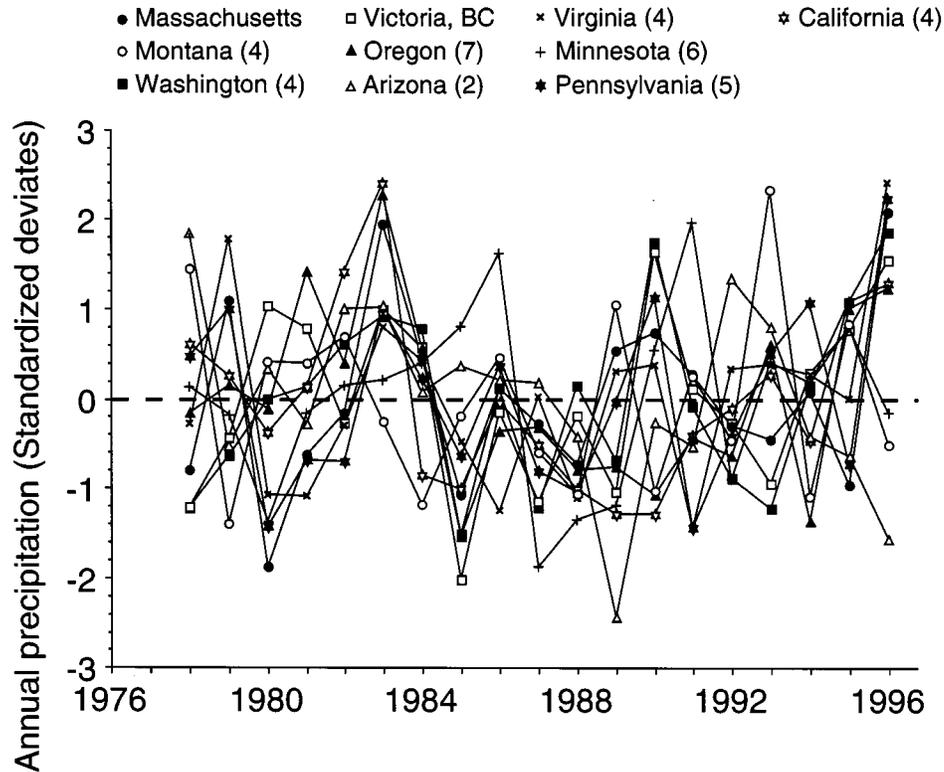


Figure 2: Annual precipitation for regions in which the insect populations were studied, in standard deviate units calculated from 1978–1996 precipitation. The dashed horizontal line is mean precipitation for each region standardized to 0. Parenthetical numbers following states are state climatic zones. Data for the United States from the National Climatic Data Center (<http://www.ncdc.noaa.gov/>) and Victoria, British Columbia, data from the Canada Meteorological Center.

habitats (the insects comprise species feeding in deciduous and temperate rain forests, rangeland, fruit orchards, high altitude riparian habitat, and successional fields and on serpentine-soil plants) and with various feeding ecologies (exophytic folivores, a phloem feeder, galls, and leaf miners). There is also little doubt that the factors responsible for the “normal” dynamics of these species vary considerably, ranging from *C. laricella*, for which dynamics are strongly influenced by a natural enemy (Ryan 1990), to *E. lasiolepis*, for which host plant quality is the dominant regulatory factor (Price et al. 1995). Our results should not be construed as a test of the Moran effect; rather, they simply reflect that climatic extremes can also synchronize changes in insect abundances even when regulatory factors differ.

The underlying mechanism for the crashes seems straightforward; all of our examples are herbivores, and the drought severely affected the growth and survival of plants (e.g., Tilman and El Haddi 1992). Higher trophic levels were similarly affected in at least some parts of North America; the specialized natural enemy complex associated with *E. solidaginis* collapsed in concert with its galler resource in Pennsylvania (Sumerford 1991), and

food web structure in temporary ponds was simplified by a loss of predators in Wisconsin (Sneider 1997).

Although no ecologist doubts that severe climate can depress insect populations, and it is unlikely that all insect populations in North America were equally affected by the drought, it is perhaps more surprising that population crashes can be so widespread geographically and involve species with a wide range of dynamics. It should be noted that some of these insects show cyclic population dynamics over longer time periods (e.g., gypsy moth, western tent caterpillar, and the grasshoppers; references in fig. 1 legend), so their crashes during the drought could be coincidental. But it remains that troughs did coincide with the drought, and the potential role of climate in their dynamics cannot be summarily dismissed. Indeed, it has been suggested that synchronization of Holarctic forest Lepidoptera population cycles are correlated with sunspot activity and perhaps cool temperatures (Myers and Rothman 1995). Even so, whereas the cause and effect relationship for these very large-scale patterns is difficult to determine, the effects of droughts are clear.

Contemporary climatic patterns suggest that transcon-

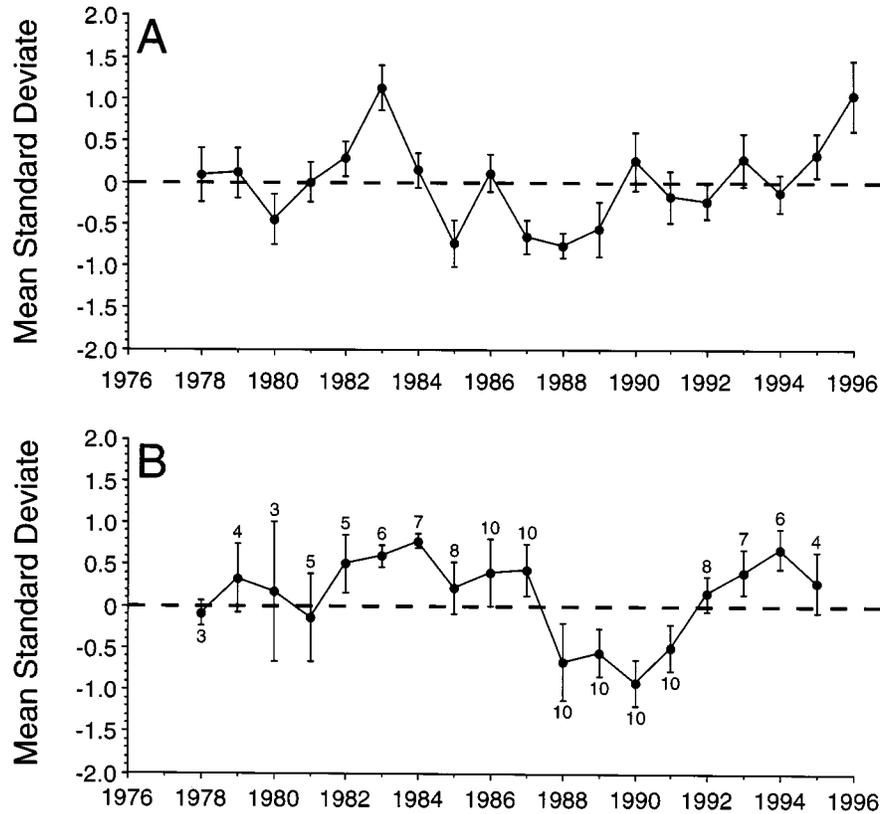


Figure 3: Mean standard deviates (± 1 SE) for (A) annual precipitation (from fig. 2) and (B) insect abundances (from fig. 1). The dashed horizontal lines are means standardized to 0. Numbers near error bars in B are numbers of cases.

tinental, synchronized population crashes occur rarely. However, global climate change may increase the frequency of extreme events (Wigly 1985; Schneider and Root 1996). If this happens, large-scale entrainment of insect populations could become much more commonplace in the future. Although the importance of density-independent factors to population dynamics has been long appreciated, they have been eclipsed by a focus on density-dependent regulation (see Turchin 1995 for a lucid review of the problem). The next century may see a need to reemphasize the role of density-independent factors in insect population dynamics, particularly at larger spatial scales.

Acknowledgments

We thank M. Auerbach, E. Connor, G. Dwyer, P. Price, and R. Ryan for assistance with their time-series data and D. Sumerford and S. Weiss for allowing us to use the data from their theses. We also thank A. Agrawal, A. Berryman, H. Cornell, I. Hanski, S. Harrison, S. Lawler, and J. Roland for their comments on drafts of the manuscript.

Literature Cited

- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Auerbach, M. J., E. F. Connor, and S. Mopper. 1995. Minor miners and major minors: population dynamics of leaf-mining insects. Pages 83–110 in N. Cappuccino and P. W. Price, eds. Population dynamics: new approaches and synthesis. Academic Press, San Diego, Calif.
- Box, G. E. P., and G. M. Jenkins. 1976. Time series analysis: forecasting and control. Holden-Day, San Francisco.
- Horton, D. R., B. S. Higbee, T. R. Unruh, and P. H. Westgard. 1992. Spatial characteristics and effects of fall density and weather on overwintering loss of pear psylla (Homoptera: Psyllidae). Environmental Entomology 21:1319–1332.
- Kemp, W. P., and B. Dennis. 1993. Density dependence in rangeland grasshoppers (Orthoptera: Acrididae). Oecologia (Berlin) 96:1–8.
- Lawton, J. H. 1995. The response of insects to environmental change. Pages 3–26 in R. Harrington and N. E.

- Stork, eds. Insects in a changing environment. Academic Press, London.
- Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian Journal of Zoology* 1:291–298.
- Myers, J. H., and L. D. Rothman. 1995. Field experiments to study regulation of fluctuating populations. Pages 229–250 *in* N. Cappuccino and P. W. Price, eds. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, Calif.
- Price, P. W., T. P. Craig, and H. Roininen. 1995. Working toward theory on galling sawfly population dynamics. Pages 321–338 *in* N. Cappuccino and P. W. Price, eds. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, Calif.
- Ranta, E., V. Kaitala, J. Lindström, and H. Lindon. 1995. Synchrony in population dynamics. *Proceedings of the Royal Society of London B, Biological Sciences* 262: 113–118.
- Ranta, E., V. Kaitala, J. Lindström, and E. Helle. 1997. The Moran effect and synchrony in population dynamics. *Oikos* 78:136–142.
- Royama, T. 1996. *Analytical population dynamics*. Chapman & Hall, London.
- Ryan, R. B. 1990. Evaluation of biological control: introduced parasites of the larch casebearer (Lepidoptera: Coleophoridae) in Oregon. *Environmental Entomology* 19:1873–1881.
- . 1997. Before and after evaluation of biological control of the larch casebearer (Lepidoptera: Coleophoridae) in the Blue Mountains of Oregon and Washington, 1972–1995. *Environmental Entomology* 26: 703–715.
- Schneider, S. H., and T. L. Root. 1996. Ecological implications of climate change will include surprises. *Biodiversity and Conservation* 5:1109–1119.
- Sneider, D. W. 1997. Predation and food web structure along a habitat duration experiment. *Oecologia (Berlin)* 110:567–575.
- Sumerford, D. V. 1991. Two studies of tri-trophic level interactions among goldenrods, *Eurosta solidaginis* (Diptera: Tephritidae), and its natural enemies. M.S. thesis. Bucknell University, Lewisburg, Pa.
- Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. *Oecologia (Berlin)* 89:257–264.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 *in* N. Cappuccino and P. W. Price, eds. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, Calif.
- Weiss, S. B. 1996. Weather, landscape structure, and the population ecology of a threatened butterfly, *Euphydryas editha bayensis*. Ph.D. diss. Stanford University, Stanford, Calif.
- Wigly, T. M. L. 1985. Impact of extreme events. *Nature (London)* 316:106–107.

Associate Editor: Ilkka Hanski