

## Paleogene insect herbivory as a proxy for $p\text{CO}_2$ and ecosystem stress in the Bighorn Basin, Wyoming, USA

**Ellen D. Currano, K.R. Kattler, A. Flynn**

Department of Geology, Miami University, Oxford OH, 45056, USA

The early Paleogene rock record of the Bighorn Basin, Wyoming, USA, preserves both long- and short-term environmental changes. In this study, we compare the response of insect herbivores to the abrupt,  $\text{CO}_2$ -driven Paleocene-Eocene Thermal Maximum (PETM, 55.8 Ma) and the gradual Early Eocene Climatic Optimum (EECO, ~53–51 Ma). A Bighorn Basin paleotemperature record for the late Paleocene through early Eocene has already been constructed (1, 2), and paleobotanical estimates are  $20.1 \pm 2.8^\circ\text{C}$  for the PETM and  $22.2 \pm 2^\circ\text{C}$  for the EECO. Although temperature changes during the PETM and EECO are well constrained, variations in  $p\text{CO}_2$  remain poorly understood. Studies of  $p\text{CO}_2$  during the PETM conclude that more than 2,000 Gt of carbon were released in the atmosphere (3), but because  $p\text{CO}_2$  of the late Paleocene is unknown, it is impossible to compare the PETM to other time intervals. Carbon dioxide levels during the EECO have been calculated using a variety of proxies; however, estimates range from 100 to 3500 ppm (as compiled in 4).

Comparing insect herbivory during the PETM and EECO both documents biotic response to different scales of environmental perturbation and also provides insight into the nature of these perturbations. Temperature and carbon dioxide affect insect herbivores differently. Warming speeds up insect metabolic rates, which decreases larval development time and reduces susceptibility to predators and parasitoids. Therefore, insect herbivore population densities are often higher during warming events. Temperature also impacts insect diversity because of its effect on insect geographic ranges. Carbon dioxide indirectly affects insects through a decrease in food quality. Plants grown in elevated  $p\text{CO}_2$  tend to accumulate more carbon and have a lower nitrogen : carbon ratio. Insects must compensate for this decrease in nutrient concentration by increasing consumption.

We studied insect herbivory on one PETM flora and one EECO flora from the Bighorn Basin. In order to establish background values of insect herbivory, we analyzed seven additional Bighorn Basin Paleogene floras that are not from intervals of high temperature or carbon cycle perturbations. We conducted insect damage censuses to measure insect damage diversity (number of damage morphotypes, standardized by sample size) and frequency (the proportion of leaves with insect herbivore damage). Leaf area removed or damaged by insect herbivores was measured on a subset of the censused leaves using Image J.

Damage diversity is highest in the EECO and then the PETM, and both are significantly more diverse than the other sites. This is unsurprising due to the strong, positive correlation between damage diversity and temperature, and likely represents the northward migration of diverse insect populations from lower latitudes. Furthermore, the PETM and EECO are marked by significantly elevated damage frequency, which likely indicates high insect population densities. Leaf area removed/damaged by insect herbivores is significantly greater during the PETM than during the EECO, and this has two possible interpretations. First, it could signify that  $p\text{CO}_2$  was significantly higher in the PETM than in the EECO. An alternate explanation is that the abruptness of temperature and  $p\text{CO}_2$  change during the PETM destabilized terrestrial ecosystems. PETM forests were highly stressed ecosystems that lacked a tight coevolution of plants and insect herbivores.

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Autor(en)/Author(s): Currano Ellen D., Kattler K. R., Flynn A.

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