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PLANT-INSECT ASSOCIATIONS RESPOND TO PALEOCENE-EOCENE WARMING

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Terrestrial plants and insects today comprise the majority of the Earth's biomass and biodiversity, and almost half of insect species are herbivores. Consequently, understanding how plant-insect associations respond to warming events is a vital component of global change studies. Nevertheless, there have been no investigations of plant-insect interactions in the context of past climate change. The fossil record offers a unique opportunity to examine plant-insect response over long time intervals through analysis of insect damage occurring on fossil plants. Deposits bearing fossil plants simultaneously provide data on host taxonomy, paleoclimate, and stratigraphy, to which insect damage data can be tied directly. In modern insect faunas, decreasing latitude is associated with several broad trends, including increased diversity per host plant and increased herbivore pressure, the latter expressed in higher attack frequency. We used insect damage on fossil plants to test for these trends at constant latitude, in the context of the Paleocene-Eocene global warming interval. We also examined whether herbivory and its increase more affected abundant hosts, as predicted by observations of extant associations, and addressed herbivore turnover. The paleobotanical record from the Great Divide, Green River, and Washakie basins of southwestern Wyoming, USA, includes diverse and abundant floral assemblages from the Paleocene-Eocene interval that contain well-preserved insect damage. Specifically, we compared two floral samples, from the latest Paleocene (Clarkforkian) and the mid-early Eocene (mid-Wasatchian) (Wilf, submitted). Both samples were originally deposited on humid, swampy floodplains, allowing an "isotaphonomic" approach that helps to factor out biases such as depositional regime, paleotopography, and past moisture levels (Behrensmeyer & Hook 1992). Previous analysis of these samples showed that from the latest Paleocene to the mid-early Eocene: (a) mean annual temperatures rose from 14.4°C ± 2.5°C to 21.1°C ± 2.2°C; (b) plant species turnover exceeded 80%; (c) all dominant plant taxa were replaced; (d) alpha, beta, and gamma diversity increased significantly; and (e) an immigration of thermophilic plants occurred (Wilf, submitted).

Presence-absence data were tabulated for 39 Paleocene and 49 Eocene species of terrestrial flowering plants at 49 Paleocene and 31 Eocene localities. Forty-two types of insect damage were identified. A database was constructed in which the presence or absence of each damage type was scored for each species in each of the two samples. In addition, we field-censused the four plant localities with highest diversity and best preservation in the Paleocene and Eocene for insect damage on dicot leaves (two each, 749 Paleocene and 791 Eocene specimens). This analysis permitted the observed damage frequencies to be related as directly as possible to the relative abundance of host plants in the source forests. The census data were analyzed first for all leaves, then separately for Betulaceae and all nonbetulaceous taxa. A single species of Betulaceae was a dominant component of the vegetation in both the Paleocene (*Corylites* sp.) and the Eocene (*Alnus* sp.). These two species fit the traditional model of "apparent" plants (Feeny 1976): abundant, conspicuous hosts that form significant ecological islands. Like all modern Betulaceae, which are heavily consumed by insects, *Corylites* and *Alnus* were thin-leaved and deciduous, adding to their presumed palatability. For these reasons, these betulaceous species were a significant fraction of the flora we hypothesize to have been frequently consumed by a high diversity of herbivores, as is the case with modern abundant taxa.

The census data indicate that overall damage frequency was significantly higher in the Eocene sample (Paleocene: 29±1.7%; Eocene: 36±1.7%), providing evidence for increased herbivore pressure. The Betulaceae were attacked significantly more often than the non-betulaceous fraction within both sampling levels, and their damage frequency increased markedly (Paleocene: 33±2.1%; Eocene: 46±3.0%). The Betulaceae, in particular, also recorded increased herbivore pressure and herbivore diversity from multiple damage frequency on single leaves, measured as the percentage of leaves with more than one damage type (Paleocene: 9.0±2.2%; Eocene: 22±3.6%). The diversity of insect damage per host species was well-correlated with host abundance, measured as the percentage of localities where a given host occurred within its sample (Paleocene: $r^2 = 0.78$, $p < 10^{-12}$; Eocene: $r^2 = 0.52$, $p < 10^{-8}$). This result is congruent with modern correlations of host abundance and herbivore diversity, although some correlation is expected simply because increased sample size raises the probability of discovery of a damage type. When abundance was held constant between the Paleocene and Eocene samples, greater herbivore diversity per host plant was found in the Eocene. The Eocene slope was higher, with separation of 68% confidence bands present above the ~25% occurrence level (damage diversity as the dependent variable, abundance the independent variable), and the five largest positive residuals were all Eocene species. The difference in slope was more marked if sampling was held constant instead of abundance: when the independent variable was changed to the absolute number of localities of occurrence rather than the percentage, the Eocene slope became double that of the Paleocene. The Eocene dominant *Alnus* sp., carried the maximum damage diversity (24), higher than the more abundant Paleocene confamilial, *Corylites* (18). As the plant with the highest herbivore diversity and attack frequency, we hypothesize *Alnus* to have been apparent and rapidly growing, with limited investment in chemical defenses. *Alnus* palatability in the Eocene was probably enhanced by elevated leaf nitrogen content resulting from an actinorhizal association with nitrogen-fixing symbionts, as in all modern *Alnus*.

The Paleocene-Eocene floral turnover appears to have accompanied a turnover in the herbivore fauna. Twenty-four percent of damage types made their last appearances in the Paleocene, whereas 28% made their first appearances in the Eocene. Many of these damage types are generalized and relatively more likely to have been produced by unrelated insects. However, if only the 27 most specialized damage types are counted, which are each more likely to correspond to restricted taxonomic groups of herbivore culprits, the results are similar: Paleocene last appearances are 26% and Eocene first appearances 33%. The observations of rare, specialized damage types are derived from intensively sampled hosts.

which supports our view that their turnover is not a sampling artifact. The percentages given above should be regarded as minima given the difficulty of evaluating turnover in more generalized feeding groups. We conclude that a Paleocene-Eocene turnover of at least 25% occurred in the herbivore fauna, in parallel with the climatic and floristic change already documented in the Rocky Mountain region.

References

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