

# This Week's Citation Classic

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**Janzen D H.** Herbivores and the number of tree species in tropical forests. *Amer. Naturalist* **104**:501-28, 1970. [Dept. Biology, Univ. Chicago, Chicago, IL]

**Relatively prey-specific seed and seedling predators may reduce population recruitment by a tropical tree species to where it cannot thoroughly, competitively dominate the habitat, thereby leaving space to be occupied by other species. The more effective these herbivores, the more species of plants should be found in the same habitat. This process is probably one of the causes of high tree species richness in the tropics. [The SCI® indicates that this paper has been cited over 145 times since 1970.]**

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"Sometime in 1966 or 1967 Cordon Oriens, who was walking behind me in the rain forest on the Osa Peninsula in southwestern Costa Rica, asked why there were so many tree species in the forest. I glibly replied that it was because the seed- and seedling-eating animals were keeping the density of any one tree species down so low that it could not competitively keep the others out even if it were a better competitor. The idea undoubtedly had many roots, including: Three to four 'years of rearing seed predators and seeing how specific and devastating many were, the impressive presence throughout the year of vertebrate and insect seed predators in tropical vegetation, the obvious difficulty of locating offspring of a given species of tropical forest tree even when it produced huge seed crops, and Bob Paine's similar description of the impact of certain predators on intertidal sessile invertebrates.

"The idea found its way into a long manuscript on interrelations of seed predators with seeds in early 1969, which Charles Michener very kindly told me should be split in two because the idea was more interest-

ing than the other data. In the fall of 1969 I had a semester to kill while waiting for a new office at the University of Chicago, and I spent the time trying to formalize a statement about 'given an m<sup>2</sup> of rain forest constantly bombarded by seeds, what determines which ones live and which ones die?' I spent nearly a month figuring out what happens if you multiply a real number curve (seed immigration with distance from the parent tree) times a probability curve (chance of survival with increasing distance from the parent tree). Then I was gently informed by Richard Levins that this was one of the final exam questions in the course he was teaching. Dick Lewontin struggled through the first draft of the manuscript three times. The first time he was elated, the second time he ridiculed it, and the third time he decided it was interesting and atrociously written. He asked me to tell him the point of the paper which I did in a ten minute monologue. He suggested that I go back and tell it likewise to the typewriter, not looking at the manuscript. I started on Friday afternoon and finished on Sunday, and that is the paper as published with a few minor changes suggested by reviewers.

"The paper is widely referred to because: (1) I was teaching heavily in courses offered by the Organization for Tropical Studies and therefore explained the idea firsthand to hundreds of the best graduate students in whole organism biology in the US; (2) I enjoy giving seminars and gave many on the subject at various universities; (3) it was published in a journal widely read by people who are sometimes prolific writers and like papers that are a mix of ideas and natural history; (4) it came early in the explosion of interest in tropical studies; and (5) it offered a simplistic idea of interest to both botanists and zoologists. The tragedy of the paper is that it is often cited by workers who have not read it and its companion papers carefully, and therefore attack what they think it said rather than what it did say, or incorrectly credit it with having 'proved' that animals are the cause of high tropical tree species richness."

1. **Paine R T.** Food web complexity and species diversity. *Amer. Naturalist* **100**:65-75, 1966.