

countries has been relatively neglected until recently, mainly due to research priorities focusing on later archaeological periods. The resulting research gap manifested as empty space in the maps of Paleolithic Europe in the textbooks I studied at university. But this empty space covers a region with an important biogeographic role — as a dispersal corridor, as well as a potential glacial refugium — for human populations in the Pleistocene, and is crucial for our understanding of human evolution and dispersals. This research ambition was already formed in my days as a PhD student and has been driving my research in Greece, conducted in collaboration with the Universities of Athens and Thessaloniki and the Greek Ministry of Culture and Sports, and funded over the last eight years by the European Research Council. It has led to important results, such as the discovery of the oldest currently known archaeological site in the country, dating to ca. 450 thousand years ago, as well as the identification of an early migration of *Homo sapiens* to Europe more than 200 thousand years before the present. These results are very exciting for me, but I hope that they are only the beginning. There is much more to be done, and I hope to continue working toward fulfilling this goal for a long time to come!

Do you believe that there is a need for more crosstalk between disciplines?

Yes, absolutely! In fact, the study of human evolution is by definition cross-disciplinary, drawing not only from biology (e.g. evolutionary biology, primate ecology and behavior, genetics) but also geology (e.g. paleontology) and the humanities (e.g. archaeology, linguistics, ethnography). While such an interdisciplinary outlook is not always easy, limiting one's perspective to only one of these components risks missing out on important insights and is bound to lead to an incomplete understanding of how humanity — in all its complexity — came to be. It is my strong belief that only through interdisciplinary work can we hope to answer big questions.

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Quick guide

Conifer bark beetles

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What are bark beetles? Bark beetles (Coleoptera: Curculionidae, Scolytinae) are small, cylindrical beetles ranging from ~1 mm-long *Hypothenemus* spp. to ~8 mm-long red turpentine beetles (*Dendroctonus valens*). They comprise a large and diverse group of insects consisting of >6,000 species worldwide. About 25 species are commonly recognized as important disturbance agents in conifer forests, particularly in North America and Europe. Bark beetles spend most of their lives within a host tree, feeding and reproducing within the bark. Trees of all species, ages, and sizes may be colonized and killed by bark beetles, but each bark-beetle species exhibits unique host preferences, life history traits, and impacts (Figure 1A).

How do bark beetles locate and colonize host trees? Adult bark beetles have very limited energy reserves, and are highly susceptible to predation, starvation, and adverse abiotic conditions while searching for hosts. Therefore, they must efficiently locate the correct habitat and host tree species, as well as the most suitable hosts, using a variety of visual and olfactory cues. Once a host is selected, pioneering beetles bore into and through the outer bark and initiate gallery construction in the phloem (that is, the innermost layer of bark that transports photosynthates). Once inside, many bark-beetle species release aggregation pheromones that enhance attraction of conspecifics. In response to this wounding, conifers release oleoresin, which exudes from the entrance hole and may encapsulate and kill pioneering beetles (Figure 1B); this response may be sufficient to thwart the attack. Successful host colonization requires overcoming these and other tree defenses, and generally requires large numbers (several hundreds to thousands) of beetles to 'mass attack' the tree over the course of several days; the healthier the tree the more

beetles are required to overwhelm its defenses.

Following mating, eggs are laid along the edges of galleries. Upon eclosion, larvae excavate feeding tunnels in the phloem and/or the outer bark (Figure 1C). Bark beetles carry a variety of phoretic organisms that may be introduced into the tree as well. The best studied are the symbiotic blue-stain fungal associates in the family Ophiostomataceae, which serve as important food sources for larvae and adults and may negatively impact tree health. However, tree mortality occurs primarily by girdling of the phloem during gallery construction and larval feeding. Following pupation, adult beetles of the next generation tunnel outward through the bark and initiate flight in search of new hosts. Voltinism varies with some species, such as the southern pine beetle (*Dendroctonus frontalis*), completing several generations per year whereas others, such as the spruce beetle (*Dendroctonus rufipennis*), take up to three years to complete a generation.

Under what conditions do bark beetle epidemics occur? Mechanisms contributing to bark beetle epidemics are complex and include density-dependent and density-independent factors. However, two requirements must be met: first, there must be favorable weather conducive to beetle survival and population growth; and second, there must be an abundance of susceptible host trees. Climate change is exacerbating some epidemics due to shifts in temperature and precipitation that influence bark beetles, their hosts, and community associates. Forest densification (for example, due to fire suppression) has also contributed to some epidemics due to increased competition among trees for water, nutrients and growing space thereby increasing their susceptibility. Bark beetles have many natural enemies, including invertebrates (such as predatory beetles, snakeflies and parasitoid wasps) and vertebrates (for example, woodpeckers), but these likely have a very limited role in regulating epidemics.

What impacts do bark beetles have on forests? Tree mortality attributed to bark beetles can influence the

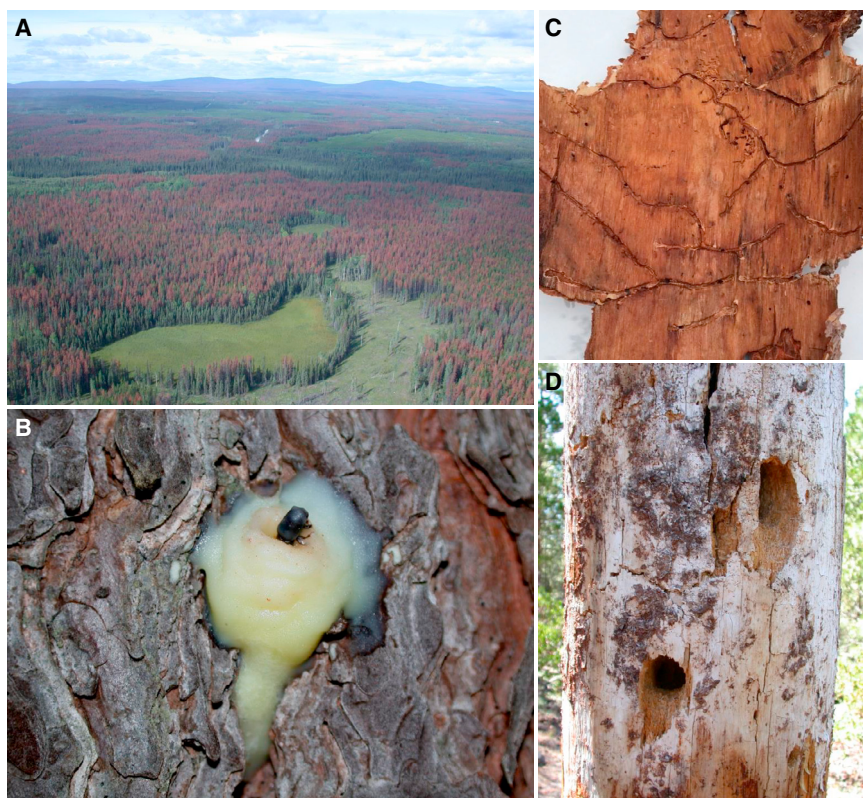


Figure 1. Conifer bark beetles are small insects capable of causing big impacts.

(A) Among bark beetles, the mountain pine beetle (*Dendroctonus ponderosae*) exerts the largest impacts and is among the best studied. The faded trees are lodgepole pines (*Pinus contorta*) colonized by the mountain pine beetle the previous summer, British Columbia, Canada, 2005. (B) Bark beetles that initiate host colonization are often killed by drowning or immobilization in oleoresin that collects at the entrance hole. In this case, the pioneering beetle is a female western pine beetle (*Dendroctonus brevicornis*) ~4 mm long. (C) *D. brevicornis* galleries in the inner bark of a ponderosa pine (*Pinus ponderosa*). In most cases, the colonizing species can be identified from the gallery patterns left behind. (D) Although we tend to focus on the negative impacts of bark beetles on ecosystem goods and services, it is important to remember their roles in the proper functioning of forest ecosystems. For example, bark beetles serve as keystone species, facilitating colonization of trees by other organisms. In this case, a woodpecker nesting cavity (round hole) is visible in an old ponderosa pine snag.

function, structure, and composition of forests by regulating aspects of primary production, nutrient cycling, ecological succession, and the size, distribution, and abundance of trees. In endemic populations, bark beetles create small gaps in the forest canopy by killing individual trees or small groups of trees stressed by age, drought, defoliation, or other factors. In this context, few negative impacts are observed (Figure 1D). However, epidemics may negatively impact timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, biodiversity, endangered species, carbon sequestration and storage, and cultural resources, among other factors. Some of the more prolific

tree-killing species cause landscape-scale disturbance. For example, recent epidemics of the mountain pine beetle (*Dendroctonus ponderosae*) in western North America resulted in significant tree mortality and impacted >27 million hectares. The nature and extent of these impacts varies considerably depending on the resources affected, how they are valued by society, and by the extent and severity of the bark beetle epidemic.

What management options are available? Several tactics are available to manage bark beetles and reduce associated levels of tree mortality. Suppression involves short-term tactics designed to address current infestations by manipulating beetle populations

and includes the use of sanitation harvests (that is, harvesting of currently infested trees and destroying the brood within these trees prior to emergence), insecticides, semiochemicals (chemicals released by one organism that elicit a response, usually behavioral, in another organism) or a combination of these and other treatments. Efficacy varies, but in general, suppression is most effective when bark-beetle populations are relatively low (for example, during the transition between endemic and epidemic populations). Prevention is designed to reduce the probability and severity of future bark-beetle infestations by manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, and/or altering age classes and species compositions.

Where can I find out more?

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