

Quick guide

**The spongy moth,
*Lymantria dispar***

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What is the spongy moth? The spongy moth is an invasive, univoltine, foliage-feeding tussock moth with a native range spanning most of the Palaearctic and an invaded range in eastern North America (Figure 1). Until recently, this insect was referred to as the ‘gypsy moth’, but in 2021 the Entomological Society of America, recognizing the derogatory nature of the word ‘gypsy’, changed the common name to be harmonised with the German name *schwammspinner* and French name *spongieuse* — both of which reference the spongy nature of the egg masses laid by female moths.

Larvae of the moth overwinter as eggs, hatch in spring, and continuously feed on leaves through early summer. The spongy moth has a remarkably wide range of host plants that varies among regions. It is known to feed on the foliage of hundreds (>300) of deciduous and coniferous tree species, including oaks, poplars, larches and pistachios. In most populations, mature larvae feed in tree crowns during the night, and in the morning crawl down to hide in bark crevices or rocks. Male larvae of *L. dispar* have five instars, while female larvae have six instars. After spending one or two weeks in the pupal stage, adults emerge, mate and lay eggs (Figure 1). In most Asian populations, females are capable of flight, whereas in North American and most European populations, females are flightless, despite having well-developed wings, and lay their eggs on tree trunks or rocks near sites where they pupated. The lifespan of an adult spongy moth is only 1–7 days, but even in this short time, a single female can lay over 1,000 eggs, so there is enormous potential for population growth. Like other moths, the spongy moth is a source of sustenance for several species of predators and parasitoids. Among





Figure 1. The spongy moth.

Top left: Spongy moth late larval stage (photo: Michael Schöne). Middle left: Spongy moth pupae attached to a twig with silk (photo: Scott A. Conner). Bottom left: Mating of a spongy moth male and female (photo: Mara Tabaković-Tošić). Top centre: Eggs and egg masses laid by female spongy moths (photo: Valery Kirsanov). Bottom centre: Manual removal of spongy moth egg masses in Massachusetts, 1891 (from Forbush and Fernald (1896)). Top right: Distribution of the spongy moth in North America. Middle right: Distribution of the spongy moth in the Palearctic. Red: *L. d. dispar*. Yellow: *L. d. asiatica*. Green: *L. d. japonica*. Bottom right: An oak-dominated forest in Hillsdale, New York that was defoliated during a spongy moth outbreak in 2021 (photo: Mark Flotterhand).

these, small mammals are known to be voracious predators of larvae and pupae, and birds have also proved to be common predators, killing larvae and damaging the egg masses of *L. dispar*. However, in certain circumstances, this impact is not sufficient, and populations may grow through five orders of magnitude in just a few years. At low densities, spongy moths can be very difficult to find, but at high densities, they can consume 100% of forest foliage (Figure 1). Defoliation of forest canopies reduces tree growth, and the reduction in leaf area also affects transpiration and water balance in trees. These changes can resemble the effects of drought on tree physiology, sometimes leading to their death.

Where does it come from and how many spongy moths do we have?

The natural history of the spongy moth and the number of its subspecies has been the subject of numerous studies. Two main geographical regions — East Asia and Transcaucasia — have been suggested as possible areas of origin of this species. While early studies suggested East Asia as the region where *Lymantria dispar* originated, the recent evidence suggests the wider Transcaucasian region as its area of origin. It appears that *L. dispar* diversified from a common ancestor in the Pleistocene and spread across the rest of the Palearctic region during the interglacials. Within this species range, considerable variation exists in traits such as body size, larval coloration and female flight capabilities.

Several attempts have already been made to classify these heterogeneous populations into subspecies. The first classification used these biological and morphological characters to identify seven subspecies of *L. dispar*. The greatest enigma since the beginning of the 20th century remained the variability of the spongy moth in the Japanese archipelago, as a total of four subspecies had previously been described from this area. Recent genetic studies support the existence of three subspecies: *L. dispar dispar* (known as the European spongy moth), which occurs in the western Palearctic, Central Asia and North America; *L. dispar asiatica* (or Asian spongy moth), which occurs in Central and East Asia; and *L. dispar japonica*, endemic to the Japanese archipelago and Sakhalin.

The success of the spongy moth as an invasive pest can be attributed not only to its strong polyphagy (which means that it can find a host plant in almost every temperate region), but also to the species' propensity to be accidentally transported by humans. Their behaviour of seeking cryptic resting sites often results in egg masses being laid on firewood and human-made objects such as on the undercarriage of automobiles. Movement on such objects is responsible for their accidental transport to new regions in North America, and also to more distant locations, such as New Zealand.

Why is there so much fuss about this moth? The human-mediated dispersal of spongy moths over long distances is more-or-less well documented historically. In 1869, the species was introduced to North America by the amateur entomologist Étienne Léopold Trouvelot, who accidentally allowed larvae to escape in his garden near Boston. He reported his accident to local entomologists, but nothing was done until 12 years later, when populations in his neighbourhood erupted, causing massive defoliation. The first ever government campaign to eradicate an insect was attempted (Figure 1) but failed, and by 1900 the species was widespread in the Boston area, causing considerable damage to forests. Since then, the species has continued to expand its North American range, which now includes 20 eastern US states and 4 Canadian provinces (Figure 1).

Along the expanding population front stretching from Minnesota to North Carolina, a joint project of U.S. state and Federal governments has been successful at reducing range expansion by over 50%. The program uses grids of pheromone traps to detect newly established populations, which are subsequently suppressed, mostly using aerial application of synthetic pheromones disrupting the mating of adult moths. In more distant locations, such as California and British Columbia, government agencies also use networks of pheromone traps (typically >100,000 traps/year) to detect new populations. Since 1970, >300 populations have

been discovered and successfully eradicated, mostly using aerial application of the microbial insecticide containing *Bacillus thuringiensis*, thereby preventing the establishment of the species in western North America.

Outbreaks in both the native and invaded range are cyclic phenomena, with outbreaks recurring every 5–10 years. Outbreaks are common in suburban areas, and residents often become upset by defoliation of their tree canopy and the large numbers of hairy caterpillars crawling in and around their homes. Also, in a small proportion of people, hairs on larvae can trigger pruritic dermatitis, also known as spongy moth rash. Consequently, residents and government agencies often resort to using pesticides to suppress outbreaks, though it is not practical to impact regional population cycles. Most broadleaf trees can tolerate typical one or two-year defoliation episodes, though tree mortality can be acute when defoliation is coincident with drought conditions. In North America alone, the total costs associated with the spongy moth are approximately US\$3.2 billion per year.

While many invasive species are innocuous in their native range, this is not the case for the spongy moth. The species exhibits outbreaks throughout its native range, with episodes of total defoliation of larch in Mongolia, pistachio and apple in Central Asia and oaks and poplars in Europe. In several countries, such as Germany, aerial spraying with chemical or microbial insecticide is carried out to suppress outbreaks, but these practices are increasingly controversial given concern about impacts of insecticides on other forest species. The impact of aerial spraying during the spongy moth outbreaks on the survival and life history of other species has been poorly studied. As a voracious herbivore, the spongy moth appears to affect not only host plants through defoliation, but also other herbivorous species that feed on the same host species. During outbreaks, populations of other herbivores may be adversely affected from changes in leaf chemistry and water content triggered by defoliation, and also by the predators and generalist

parasitoids whose abundance increases with outbreaking spongy moth populations.

Are there recent or expected future changes in spongy moth status?

The status that any species maintains in the community in which it is embedded is often not static, and this is also the case with the spongy moth. Evidence suggests that when the species was first introduced to North America, it exhibited sustained outbreak densities. But in the early 1900s, the entomopathogenic nucleopolyhedrosis virus, specific to the spongy moth, was accidentally introduced with parasitoids imported for purposes of biological control. While these parasitoids may have exerted some regulation of populations, the establishment of the virus came to play a dominant role in the dynamics of North American spongy moth populations. This virus is typically the cause of collapse of outbreaks in populations around the world, and following its release, North American populations settled into the same oscillatory dynamics seen in much of Europe and Asia. The next shift in population dynamics came when the entomopathogenic fungus *Entomophaga maimaiga* was accidentally introduced to North America and caused a regional crash in outbreak populations in 1989. Before that time, this fungal pathogen was only known from spongy moth populations in east Asia, but following its emergence in North America, outbreaks declined in amplitude. A similar decrease in the extent and intensity of outbreaks has been observed across much of Europe following the introduction and spread of *E. maimaiga* from Bulgaria in 1999.

Given such historical shifts, it can be anticipated that more changes may be in store for the spongy moth in the future. With the trend of climate warming, it is expected that its geographical range and the extent of its outbreaks will slowly shift northwards. Furthermore, it can be anticipated that given trends of increasing international trade and travel, the species will continue to expand its range, both in North America, and into new continents where it currently is not established.

Considering this species' tendency to exhibit wide population swings, it may be likely to cause extensive damage in many of these new areas and continue to be subject to intense management and research in the future.

Where can I find out more?

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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