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Cycles and importance of the larch budmoth

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The grey larch budmoth (*Zeiraphera griseana* [Hübner]) is a small moth that became internationally famous for its periodic, large-scale infestations of larch forests in the Engadine (Fig. 1) and other inner Alpine valleys in Europe. While public attention remains limited to the years when regional outbreaks occur, this moth has become one of science's best-known examples of cyclic population fluctuations.

Fig. 1. At the culmination of the roughly nine-year cycle, larch trees infested with larch budmoth larvae turn reddish brown. The cembran pine trees in the foreground are unaffected.

The first historical mention in Switzerland of a "disease" that turned extensive larch forests yellow-brown dates from 1820 in the municipality of Ardon in Valais (Coaz 1894). A little later, in 1829, an entry in the annual report of the Swiss Alpine Club (SAC) stated that both sides of the Lötschental valley were desiccated and fox red in colour. Yet the true cause of this observed phenomenon was only identified in 1857, when a forestry inspector named Albert Davall brought the moths to the attention of his fellow foresters (Davall 1857). Davall attributed the "devastation" of larch trees from Sion to Upper Valais and in the side valleys to the larvae of "*Tortrix pinicolana*". The alleged reason for their mass emergence was the Valais region's meagre populations of songbirds, which had been decimated by bird hunting in neighbouring Italy. There were also observations of discoloured larch stands covering the slopes of the Upper Engadine in midsummer every few years. The first record of this phenomenon in Grisons, in the municipality of Zernez, dates back to 1855, and in 1894 Switzerland's senior forestry inspector at the time, Johann Coaz, first described cyclic gradations (mass outbreaks) in the Upper and Lower Engadine and in the Münster valley (Coaz 1894). Further outbreaks were documented in the Albula region, in Davos and even on the northern edge of the Alps at the mountain Calanda near Chur. For a long time, these mass outbreaks were thought to pose a serious threat to larch forests because they often resulted in the die back of many trees.

In the mid-20th century, when tourism in Switzerland slowly started picking up again after the Second World War, another larch budmoth outbreak was in full swing. Consequently, the tourism industry in the Engadine pushed for the application of DDT, considered a wondrous new insecticide at the time, to treat the unsightly forests. Indeed, DDT was subsequently applied on a trial basis in the Goms district of Valais. In 1948, the pressure to apply insecticides set in motion a long-term study spanning six decades, driven primarily by Werner Baltensweiler at the Swiss Federal Institute of Technology (ETH Zurich). In the course of this ongoing study, more than 130 scientific papers were produced, changing the public and scientific perception of the larch budmoth as a mere pest to an ecosystem engineer and fascinating topic of study.

The biology of the larch budmoth

The larch budmoth occurs all over Central and Northern Europe and its range extends as far east as Siberia. It is a small, speckled grey-brown moth with a 2 cm wingspan, and it belongs to the family of leaf rollers (Tortricidae, Fig. 2). Its larvae reach a length of 1.5 cm and occur in a range of colours. There are two ecotypes of the larch budmoth: The larch form has a black head capsule and is initially light in colour but later turns grey-black (Figs. 4a–c), whereas larvae of the yellowish-grey cembran pine form have an orange-yellow head

Fig. 2. The grey larch budmoth.

Fig. 3. When a mass outbreak occurs, the caterpillars restlessly wander across the twigs and branches, feeding lightly on large numbers of needles rather than completely devouring them, and leave behind faecal crumbs and spun silk threads. The desiccated needles cause widely visible discolouration of the tree crowns.

capsule (Fig. 11). The biology of the larch budmoth was studied in detail in the Engadine (Maksymov 1959). Its eggs overwinter in diapause under lichen or scales of cones or bark. The young larvae hatch in mid-May and feed first on the short shoots inside fresh needle clusters (Fig. 4a). In the third and fourth larval instar, the caterpillar feeds in an open-topped case, spun together out of a cluster of needles (Fig. 4b). When the needles it bites into start drying out, the caterpillar moves on to a fresh cluster. In early July, the caterpillar enters its fifth and final larval instar. It starts off by eating away the tip of its needle case, then constructs a web along the branch axis and, from inside this shelter, feeds laterally on other needle clusters (Fig. 4c). This is the most destructive stage because the larva often just gnaws on the needles, repeatedly moving from one cluster to another as the bitten needles start to dry out (Fig. 3). A single larva needs between 10 and 20 clusters of needles for its development, but it eats just half their needle mass (so-called wasteful feeding). When a mass outbreak occurs, the dried-out needles make the larch stands turn reddish brown, starting in mid-June, though the actual extent of discolouration also depends on precipitation. Larvae that run out of food on one branch wander elsewhere on their host tree or spin filaments and lower themselves down onto lower-lying branches. This leaves a tangle of spun threads in the crown and on the trunk of an infested larch tree. At the end of its roughly four-week development, the larvae lower themselves to the ground on a thread or by free-falling and enter their one-month pupal phase in the litter layer (Fig. 4d). The moths emerge from the end of July to September, swarming between dusk and midnight during summer and around noon under the cooler conditions during late autumn. Mating takes place during these flights, and the females then lay up to 300 eggs over a three-week period, depending on the cycle phase.

As mentioned above, the larch budmoth has another form that can develop not only on larch but also on cembran pine, Scots pine and spruce trees (see the section entitled "Fitness of different ecotypes"). On cembran pines and spruce, the larvae only feed on the young needles of fresh shoots formed that year and therefore cause no noticeable discolouration. Larger-scale outbreaks of larch budmoth larvae are also known to occur in spruce stands in Eastern Europe (Baltensweiler 1966). These infestations severely weaken the trees, making them vulnerable to bark beetle infestations.

Fig. 4. Development of the larch budmoth: the young larvae first feed on the young needles inside a spun-together cluster of needles (a). Later on, they feed on clusters of needles from the tip (b). In their final stage of development, they move along branches, protected by spun webs, feeding on needle clusters from the outside (c). Once fully developed, the larvae drop to the ground and pupate in the litter layer (d).

Natural enemies

In the 19th century, the larch budmoth's main natural enemies were thought to be birds, especially tits, prompting Coaz (1894) to lament the hunting of migratory birds in Switzerland's southern neighbour Italy. Songbirds do indeed consume large numbers of caterpillars when there is a mass outbreak of larch budmoth larvae, as does the Scottish wood ant *(Formica aquilonia)*, which is common in the Engadine. These ants mostly prey on older larvae outside their needle cases and on pupating caterpillars on the ground. However, more voracious natural enemies of larch budmoth larvae include a wide variety of parasitic wasps and flies (Delucchi 1982), which parasitize larch budmoths at all stages of their development (eggs, caterpillars and pupae). The main parasitoids at the larval stage are three species of chalcid wasps – *Sympiesis punctifrons, Dicladocerus westwoodii* and *Elachertus fenestratus* (Eulophidae) – and the ichneumonid *Phytodietus griseanae* (Delucchi 1982). In addition, during the larch budmoth's nine-month-long egg stage, the eggs are attacked by predators like mites or plant bugs (Delucchi *et al.* 1975). In addition, there are sporadic outbreaks of diseases, such as viruses.

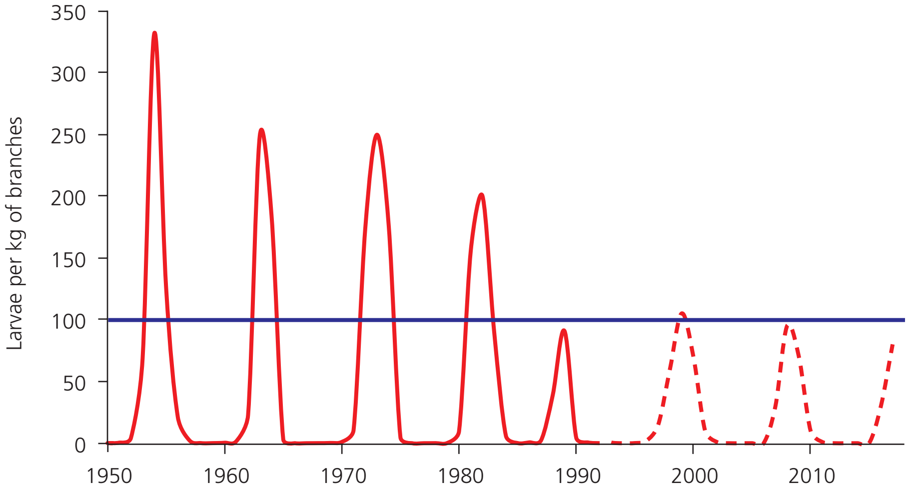

Fig. 5. Cyclical population fluctuations of the larch budmoth in the Upper Engadine. The mean periodicity is 8.5 years and the threshold for visible discolouration of larch stands is 100 larvae per kilogram of branches (blue line). The solid red curve is based on data from Baltensweiler (1993a) and Baltensweiler and Rubli (1999). The dashed line is based on visual estimates made in the field.

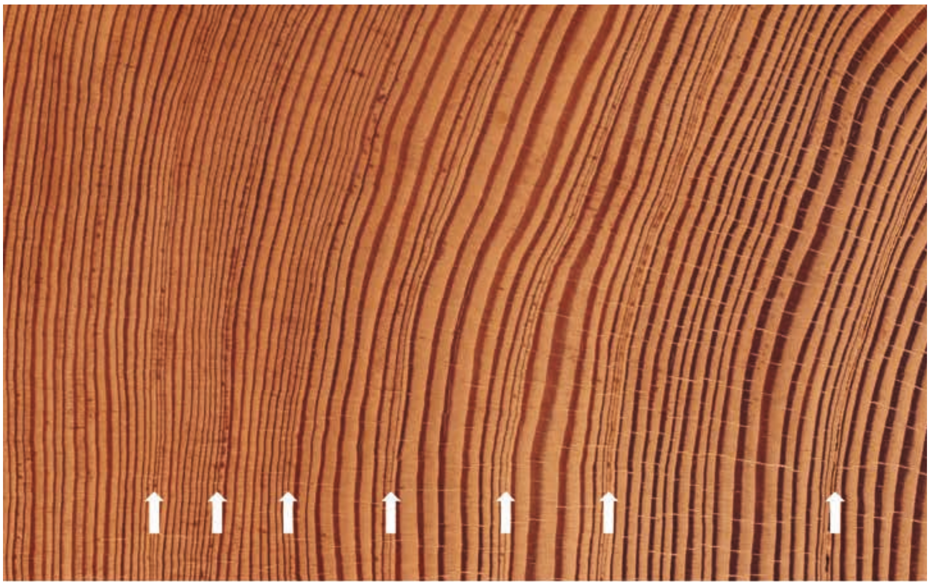

Fig. 6. Outbreaks of the larch budmoth are often visible in the regularly recurring, narrow annual tree rings in the stems of older larch trunks.

Population cycles

In lower elevations of the Alps and on the Swiss Plateau, larch budmoth populations always remain small and thus inconspicuous. Only in higher valleys with a more continentally influenced climate do mass outbreaks occur at more or less regular intervals.

An intensive study of the population dynamics of the larch budmoth, focusing on the Upper Engadine, was started in 1949 (Fig. 5). It emerged that outbreaks tend to occur, on average, every 8.5 years (Baltensweiler and Fischlin 1988). Within four to five generations, population density (abundance) fluctuates by a factor of up to 30 000! At the peak of an outbreak, there are more than 20 000 larvae on a single larch tree, and the sound of their faeces falling to the ground is audible. The trees are then criss-crossed by the threads spun by the larvae, which allow the wind to carry them to other branches or trees in their quest for new sources of food. Their population builds up and collapses again in just a few generations. During a collapse, the larval mortality rate owing to antagonists, competition and starvation peaks at 99.98 % (Baltensweiler and Fischlin 1988).

The discolouration of larch stands only becomes visible at a threshold of about 100 larvae per kilogram of branches and with 10 % of the needles being damaged (Auer 1975b). By the mid-1980s this threshold was regularly being vastly exceeded (see the section "Climate change and larch budmoth cycles").

The regular cycles in the Engadine are limited to the optimum larch budmoth habitats, situated between 1700 and 2000 m a.s.l., and to forests with a sufficiently large proportion of larch trees (Hartl-Meier *et al.* 2017). Likewise, Davall's 1857 description of the phenomenon in the Upper Valais stated that the slopes only turned red at an elevation of around 1700 m a.s.l. These cycles are not limited to the Upper Engadine, Goms and a few side valleys in Valais. They occur across the entire Alpine arc, from the French Maritime Alps to Carinthia in

Austria. There have also been occasional mass outbreaks in the Canton of Grisons in areas opening up to the north – Albula valley, the Oberhalbstein, Avers and the Domleschg – as well as in the Davos region and in Val Poschiavo (AUER 1975a).

Reconstructing historical cycles

As a tree species that sheds its needles in winter, larch can compensate for losing needles by drawing on reserves stored in its wood to produce fresh clusters later in the summer. However, their growth in years when infestations occur is severely stunted, and this is reflected in narrower tree rings in their stems (WEBER 1997 BALTENSWEILER *et al.* 2008). During such years, tree rings contain fewer early-wood cells, whereas the late wood contains just a narrow band of thin-walled cells. Larch stem discs from the Upper Engadine or larch beams from old wooden houses in the Valais often have narrow tree rings every 8 to 10 years (Fig. 6), corresponding to larch budmoth cycles. Studies have shown that larch budmoth larvae can reduce stand biomass by 1130 kg/ha during the four years following an outbreak (PETERS *et al.* 2017). Larch budmoth cycles have occurred for a very long time. In dendroecological studies carried out in the Valais, wood samples taken from living larch trees and from beams in historic buildings were used to reconstruct larch budmoth cycles spanning 1200 years; during that period, outbreaks occurred every 9.3 years on average (Fig. 7; ESPER *et al.* 2007). Whilst the intensity of outbreaks varied over the studied period, the cycle frequency remained astonishingly consistent. Even the warmer Middle Ages (6th–15th century) and the so-called Little Ice Age (15th–19th century) had no impact on this pattern.

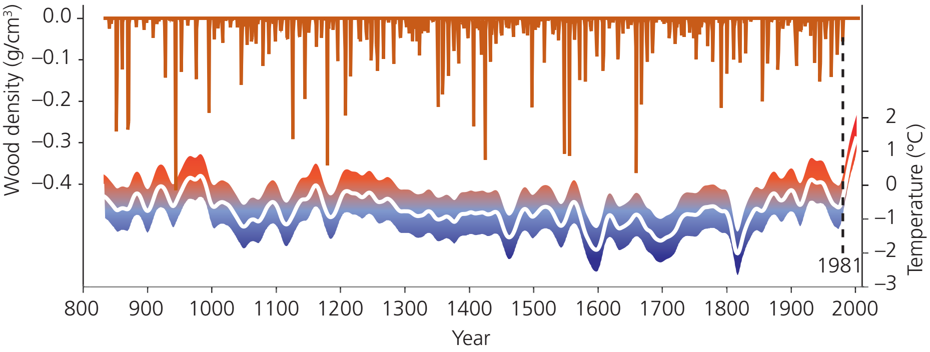

Fig. 7. Cycles of larch budmoth populations in the Valais were reconstructed by analysing tree-ring density in larch trees. The orange lines at the top show the difference in wood density between infested and unaffected trees as a measure of the severity of an outbreak. The band in the lower section of the figure shows mean temperature deviations from 1961 to 1990 (modified from ESPER *et al.* 2007).

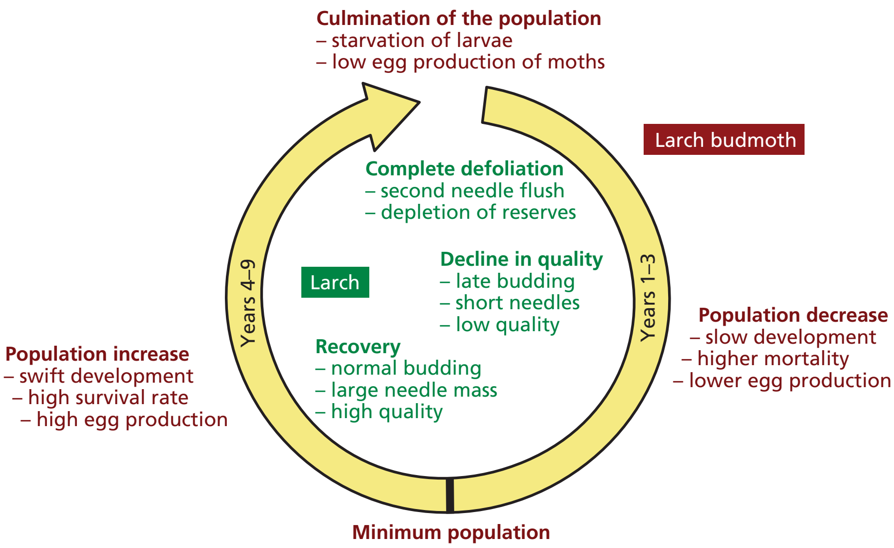

Fig. 8. The nine-year model cycle of interactions between the larch budmoth and its host tree.

What governs larch budmoth cycles?

The astonishing regularity of larch budmoth cycles begs the question of the mechanisms that cause them. In the first detailed study of an outbreak cycle in the Engadine, larvae were found to be infected by a virus as their population collapsed. This virus was deemed to be the key factor driving the population's dynamics until the next mass outbreak. In subsequent outbreaks, however, viral infection barely played a role, and several other processes were discovered that occur during mass outbreaks and shape cycles.

The negative feedback of needle quality

Larval development is closely related to larch needle quality (Fig. 8). These interactions have been intensively investigated (Benz 1974).

At the peak of an outbreak, larch budmoth larvae face strong intraspecific competition. The majority of the trees' needle mass is eaten or the needles dry up after the larvae feed on them (Fig. 3). As a result, their food source is exhausted, their mortality rate rises and the few moths that develop produce markedly fewer eggs in the autumn.

The loss of green needle mass means larch trees produce a smaller amount of photosynthates for their growth and reserves. If they lose more than half their needle mass, they bud again at the end of July, producing a second set of needles (Fig. 9). However, they do so at the expense of their reserves, which cannot be fully replenished by autumn through photosynthesis of the new needles. To compensate for losing their reserves, in such years larch trees delay shedding their needles until the late autumn. At the same time, they run the risk of losing the still green needles to early frosts before their nutrients and carbohydrates have been safely transferred to the trees' wood and roots, which can withstand winter conditions.

Further, the feeding activity of larch budmoth larvae causes cyclical fluctuations in the quality of larch needles, as low reserves due to feeding cause trees to flush their needles later the following spring and cause the needles to grow more slowly and remain between 30 and 70 % shorter. The needles additionally have a higher raw fibre content, which makes them more difficult to digest, and tend to contain less protein and nitrogen than in years without mass outbreak. As with all leaf-feeding caterpillars that overwinter at the egg stage, the timing or degree of synchrony between needle budding and the emergence of the young larch budmoth larvae is crucial. In the years after a mass outbreak, the synchrony of these events worsens and larvae emerging at the usual temperature-triggered time miss fresh, tender, readily digestible larch needles. As a result, at least the earliest larch budmoth larvae of the new population end up starving. Those larvae that do survive find needles of inferior quality that are difficult to digest and have a lower nutritional value. As a result, they grow more slowly, gain less weight and have a higher mortality rate. Moreover, the moths that develop from these larvae produce up to 90 % fewer eggs. This delayed negative feedback triggers a drastic decline in the moth population density.

It takes about three years for larch trees to recover from an outbreak. The larch budmoth population then thrives on higher-quality food and its population increases again. These interactions between the larch budmoth and its host tree also play a key role in further drivers of the cycle, as described below.

Fig. 9. Larch trees that lose more than half their needles flush new clusters of needles at the end of July when the fully developed larvae are already pupating on the ground.

Fig. 10. A larch bud moth larva with the egg of an ichneumonid parasitic wasp attached to it. Parasitic insects are one of the key factors controlling the larch budmoth cycles.

Regulation by natural enemies

The most important natural enemies of larch budmoth larvae are parasitic wasps and flies (Fig. 10), of which more than 100 species are known (Delucchi 1982). Species assemblages vary with elevation and the cycle phase. The mortality rate among larch budmoth larvae caused by parasitoids is mostly less than 10 % at the start of an outbreak, rises to 20 % at the culmination of the outbreak, and is as high as 80 % when the population collapses (Baltensweiler 1968, Delucchi 1982). The cycles of the natural enemies of larch budmoth larvae lag about two years behind those of the larch budmoth itself. Newer models involving time series analyses show that a simple host-parasitoid model, analogous to a predator-prey model, can explain 90 % of larch budmoth growth rates (Turchin *et al.* 2003). Incorporating the impact of needle quality discussed above slightly improves the model's match with data collected in the field (Iyengar *et al.* 2016, Turchin *et al.* 2003). The observed phase shift is typical of oscillating predator-prey relationships (Lotka-Volterra's law). This pattern demonstrates how important parasitoids are in controlling larch budmoth cycles.

Fitness of different ecotypes

The larch budmoth has two genetically different ecotypes (varieties): the larch form and the cembran pine form. The larch form's grey-black caterpillars feed almost exclusively on larch needles and exhibit a very high mortality rate on cembran pine. Its eggs develop significantly faster and larval mortality on high-quality larch needles is lower than for the cembran pine form (DAY and BALTENSWEILER 1972). Due to its faster egg development, the larch form is also better adapted to the timing of needle emergence (synchrony) of larch trees, which produce clusters of needles about two weeks earlier than cembran pine. Furthermore, the larch form's egg production exceeds that of the cembran pine form.

The yellowish-grey caterpillars of the cembran pine form (Fig. 11) mainly feed on new shoots of cembran pine, but they also occur on larch, Scots pine and spruce. The cembran pine form develops much more slowly and produces fewer eggs than its larch counterpart, but survives better than the larch form on poor-quality larch needles. The fitness of the larch and cembran pine ecotypes therefore differs, and the moths of the two forms even respond to different pheromones (GUERIN *et al.* 1984). Intermediate (or transitional) forms also exist between these two ecotypes that can thrive on both larch and cembran pine.

The dominance relationship between the two ecotypes changes during a cycle. At the onset of a mass outbreak, the darker larch form predominates at 80 %, developing faster than the cembran pine and intermediate forms on the initially high-quality larch needles. After complete defoliation at the culmination of an outbreak, budburst of the larch trees is delayed and they produce needles of inferior quality. At this point, the later-emerging cembran pine and intermediate forms, which survive better than the larch form on such needles, have an advantage and their percentage rises to 80 %. But since the reproductive performance of both these forms is low, the overall density of budmoths occurring on larch trees continues to decrease. Only when needle quality has improved does the fitter larch form prevail again and the reproduction rate of the population increases once more (BALTENSWEILER 1993b).

In some Alpine regions, the cembran pine has its own cycle of light-coloured larch budmoth larvae, running synchronously with and with the same periodicity as its larch counterpart (DORMONT *et al.* 2006). Since these larvae on cembran pine only feed on the needles of new shoots and thus, unlike the larch ecotype, do not trigger new needle flushing, they are not influenced by a negative impact of food quality. This also highlights the important role of parasitoids in controlling the cycle.

Moth migration and dispersal

During an outbreak, larch budmoth populations migrate locally but also disperse over a wide area (BALTENSWEILER and RUBLI 1999). If complete defoliation occurs in ideal habitats, subsequent generations of moths move on to lower-lying areas, where the larch trees were spared excessive larval feeding, to lay their eggs. Once the trees have recovered, moths fly to higher elevations over the next few years in the evenings against prevailing valley winds, thus returning to the optimum habitats characterised by better synchrony. This is the region where cycling with regular intervals is most evident.

At a larger spatial scale, the windborne dispersal of larch budmoths between inner Alpine valleys is important. In areas where larch trees have been largely defoliated by an outbreak, moths leave in large numbers and are blown into neighbouring valleys by the prevailing westerly wind. This is why the cyclical fluctuations of larch budmoth populations occur not only in the Valais and Engadine, but also in many other valleys in the European Alpine arc (Fig. 12). However, cycles are staggered over time. The first outbreaks can be observed in the valleys of the French Maritime Alps (Briançonnais). The larch budmoth culminations are then displaced at a speed of 200–300 km per year (JOHNSON *et al.* 2004), moving some 600 km to the east over the Alpine arc to the Aosta valley, Valais, Engadine, Valtellina, Dolomites and Styria. The temporal shift of outbreaks takes three to four years. Light and pheromone traps set up across the entire Alpine region have shown that countless moths are carried via Alpine passes into neighbouring eastern valleys and also onto the Swiss Plateau, where they boost local populations (BALTENSWEILER and FISCHLIN 1979, BJORNSTAD *et al.* 2002). As a result, the populations of the various Alpine valleys are closely related genetically (DELAMAIRE *et al.* 2010).

Within the Alpine arc, there are two "epicentres" with a certain momentum of their own, which superimpose their own propagation waves on the movements of the general west-to-east shift. These epicentres are the Briançonnais zone in France (Fig. 13) and the Engadine/Vinschgau in the eastern Alps (BALTENSWEILER and RUBLI 1999, JOHNSON

Fig. 11. Unlike the larva of the dark larch ecotype of the larch budmoth (see Fig. 4c), the light-coloured cembran pine form has a yellowy-orange head capsule. The cembran pine form also has a lower reproductive potential than its larch counterpart.

The larch budmoth cycles in a nutshell

The regular cycling of larch budmoth population density can be attributed to several factors. A cycle roughly develops as follows:

The synchrony between larch tree budding and the hatching of young larch budmoth larvae is best in habitats at higher elevations (1700 to 2000 m a.s.l.), where the moth populations start to increase. Most larvae belong to the dark larch budmoth form with high ecological fitness. At such times, the regulation of larch budmoth populations by parasitic insects cannot keep pace with the increase in larvae numbers, which can increase by more than twentyfold each year. At the culmination of an outbreak, the large quantities of larvae completely defoliate their host trees, which in turn causes many larvae to starve and surviving female moths to lay fewer eggs. In the following years, larch needles are of considerably lower quality and emerge later, which favours the cembran pine and intermediate forms of the budmoth that also feed on larch needles. However, high overall larval mortality and the moths' limited reproduction lead to a decline in larch budmoth populations. Furthermore, larger populations of parasitic insects exert their full, devastating effect at this point, causing the larval mortality rate to reach almost 100%. Many moths migrate to lower-lying areas, where the food available to them in the following year is of higher quality but where their offspring experience poorer synchrony with the budburst of their host tree. A high proportion of the moths are transported by westerly winds into adjacent Alpine valleys, prompting a wave of outbreaks to move from west to east across the Alps. After three to four years, regional larch budmoth populations bottom out, and larch needle quality and timing of emergence return to normal values again. By this time, the populations of parasitic insects have collapsed because of a dearth of available hosts, and the moths migrate back locally from lower-lying areas to their optimum habitats. The light-coloured cembran pine form's larvae then fade into the background, replaced once again by the larch form of the larvae, which proliferate more readily.

Overall, the fundamental mechanisms driving the cycle operate at the local scale, being based mainly on regulation by natural enemies and the negative feedback of larch needle quality as a food source. The large-scale windborne dispersal of moths across the Alpine arc stabilises and synchronises larch budmoth cycles. These mechanisms are explained in more detail in the text.

Fig. 12. At the culmination of a budmoth outbreak, larch forests turn reddish brown in midsummer. The moths then leave the affected areas and are transported eastward by wind into neighbouring valleys. This causes a west-to-east wave of infestations, starting in the French western Alps and ending about four years later in South Tyrol and Carinthia. Historical photographs from 1964 to 1979 from a) Val Guisane, France; b) Saas valley, Valais; c) Engadine, Grisons; and d) Valle Aurina, Italy.

et al. 2004, Saulnier et al. 2017). These areas are characterised by high connectivity, i.e. proximity of favourable habitats with only a few unfavourable habitats in between (Johnson et al. 2004).

Climate change and larch budmoth cycles

The maximum population densities during the last three cycles (1989, 1999, 2009) did not reach even half the previous values in the Engadine (Fig. 5), which is why in most places the larch forests were spared widespread discolouration. In France as well, far lower maxima were reached during this period. Nonetheless, the roughly nine-year periodicity of outbreaks was not disrupted in either of these areas, although defoliation was far less pronounced. In the Valais, only very little infestation was visible during this period, apart from a single, isolated outbreak in the Matter valley, and as a result there has been no reduction in annual tree ring density in the Valais since 1981 (Fig. 7). The reasons for lower maxima in recent cycles are unclear but are probably related to rising temperatures over the last few decades (Johnson et al. 2010). Warmer autumns and milder winters increase the respiration of overwintering eggs which could cause their energy reserves to become exhausted prematurely (Baltensweiler 1993a). More importantly, the crucial synchrony between larval hatching and the emergence of needles may have worsened in the spring. If larvae starve because they hatch before the needles emerge, this has a major impact on population density. Higher summer temperatures over the past 30 years probably also led to higher egg mortality during subsequent winters (Baltensweiler et al. 1971). In addition, annual ring analyses show that, during the past two centuries, the maximum intensity of infestation across the entire Alpine arc shifted to higher elevations whenever temperatures rose (Johnson et al. 2010, Saulnier et al. 2017).

Fig. 13. After three larch budmoth cycles and almost 40 years without any widespread discolouration of larch forests, in 2016 an outbreak wave with clearly visible infestations began in the French Maritime Alps (Barcelonette).

The importance of the larch budmoth

Whereas older literature describes the larch budmoth as a real pest (Coaz 1894), intensive research has significantly relativized such a negative categorisation. Since larch trees can flush new needles in late July after suffering severe feeding damage, they can at least partly compensate for reduced photosynthesis resulting from the damage. That said, doing so results in a loss of wood growth, and in dry years larch trees sometimes die after being completely defoliated (Baltensweiler et al. 2008). However, studies in the Upper Engadine have shown that fewer than 1 % of larch individuals usually die because of an outbreak and that their loss of growth is negligible (Baltensweiler and Rubli 1984). Lengthy tree-ring series (Fig. 7) show that larch trees and the larch budmoth have co-existed for millennia.

In the mid-20th century, the main fear was that discolouration of larch trees would reduce tourism (Auer 1974; Fig. 15), yet no such adverse effects are known.

Larch trees are highly dominant in many places today because, as a pioneer species, they have been able to benefit from previous disturbances. For instance, in the Middle Ages many spruce/cembran pine forests were cut down, the war years were characterised by conflagrations, and cembran pine has been deliberately targeted for use as wood panelling since time immemorial. In addition, up until the end of the 19th century the regeneration of these two tree species suffered as a result of wood pasture and mulching (Coaz 1894 Baltensweiler and Rubli 1984). These human activities enabled larch, a fast-growing, light-demanding, pioneer tree

Fig. 14. At the culmination of an outbreak, larch budmoth larvae lower themselves from their completely defoliated host trees and damage young cembran pine and spruce trees in the understorey.

Fig. 15. Although infested forests look ”diseased” to the layman, this millennia-old phenomenon is a natural process in the dynamics of larch and cembran pine forests. Only a few trees usually end up dying as a result of outbreaks. (Val Bever 1999).

bran pine trees are weakened and part of their leading shoot frequently dies, causing treetop deformations. These weakened trees are also often infested by weevils such as *Pissodes pini* or by bark beetles and plant lice. Larch trees can then capitalise on the death of cembran pine individuals, making use of newly available space and a greater incidence of light. These processes limit the development of cembran pine trees in the optimum larch budmoth habitats and thus delay the transition of larch forests to mixed larch and pine climax forests. Consequently, the larch budmoth is of great ecological importance to inner-Alpine larch forests.

Naturally, the temporary complete loss of needles at the culmination of an outbreak also affects other needle-eating insects, such as butterfly caterpillars or sawfly larvae, which almost

species, to establish a firm foothold. However, a dense, old larch forest barely regenerates, and shade-tolerant species such as cembran pine and spruce establish and ultimately form a climax forest in the absence of any new disturbances.

During recurrent larch budmoth outbreaks, cembran pine and spruce growing in the understorey are repeatedly damaged (Fig. 14). As the cembran pine form of the larch budmoth only feeds on the needles of fresh annual shoots, the main damage to this tree species is caused by larvae of the intermediate larch form, which also feed on older needles (Baltensweiler and Rubli 1984). When larch trees have been completely defoliated, the larvae lower themselves to the ground and end up on the cembran pine trees in the understorey. While larch trees can compensate for being stripped of their needles by rebudding, cembran pine can only do so to a very limited extent, so any affected parts of their crowns die back. The severest damage is suffered by cembran pine trees less than 5 m tall (Baltensweiler and Rubli 1984). Studies on the mass outbreak of the larch budmoth in 1972 showed that half the pine trees defoliated by more than 90 % were dead two years later, with further fatalities probably sustained in subsequent years (Baltensweiler 1975). Above all, young trees that are completely defoliated die immediately. Older cem-

Possible sources of confusion

In addition to the larch budmoth there are a number of other factors that can cause marked discolouration to the crowns of trees growing in mountainous areas.

- **Late frost:** If a late frost occurs in the spring, the crowns of larch trees turn yellow because their needles or needle tips freeze. Mostly only the needles of early budding short shoots are affected. The long shoots that develop later are often spared. The larch trees recover by producing new shoots much sooner than after a budmoth infestation.
- **The larch case-bearer** *(Coleophora laricella):* The larvae of this small moth mine larch needles, which constitute its food source. It tends to prefer colonising larch trees in sunny locations (e.g. on the edges of forests). The lower half of the crown is often slightly more strongly infested. The older larvae build a protruding case about 3 to 4 mm long out of hollowed needles to protect themselves. This is a characteristic feature for diagnosis.
- **Nun moth (aka black arches)** *(Lymantria monacha):* Vor allem im Wallis kommt es gelegentlich zu einem sichtbaren Nadelfrass durch die Raupen der Nonne. Meist bleibt dieser auf wenige Hektaren beschränkt. Die bis zu 6 cm langen, grauweiss gefleckten Raupen produzieren grosse Kotpartikel, die bei einem Massenbefall den Waldboden bedecken.
- **Spruce adelgids** (*Adelges* spp., *Sacchiphantes* spp.): Some species of these adelgids switch their host tree, alternating between spruce and larch. *Adelges geniculatus* only develops on larch trees. The sucking action of these insects deforms the needles, causing discolouration at the resulting kinks. Another characteristic feature of these aphids is their white wax-wool secretions, which primarily serve to protect their eggs.
- **Needle fungi:** Two fungal diseases in particular, Meria needle cast (caused by *Meria laricis*) and larch needle blight (caused by *Mycosphaerella laricina*), can discolour larch crowns in the summer. Under magnification, small spots and fungal fruiting bodies are visible on the affected needles. Clear infestations usually only become apparent in midsummer. Affected larch trees usually no longer produce fresh needles afterwards.

For more information (in German), see www.wsl.ch/diagnoseonline completely disappear in the peak years of a larch budmoth outbreak (Lovis 1975). Accordingly, the larch budmoth significantly influences the insect fauna in affected larch forests.

Control measures

As stated above, when larch budmoth larvae feed on larch trees, the negative effects remain minimal and hence do not justify the implementation of any control measures. However, for scientific reasons, in 1963 larch forests in Goms and France were treated with DDT and other insecticides on a trial basis. The impact of these substances remained limited to a single season and did not affect larch budmoth cycles (Auer 1974) because the moths' extensive dispersal replenished the decimated populations. In principle, pesticide use is prohibited in Swiss forests today.

During heavy infestations, it is important to promptly explain to the local population and holiday guests why the forests are turning brown and to promote an understanding of this spectacular phenomenon.

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