# THE FOLIVORE GUILD ON LARCH (LARIX DECIDUA) IN THE ALPS

W. BALTENSWEILER

Institute of Plant Sciences, Division of Phytomedicine
ETH-Zentrum/CLS
CH 8092 Zürich, Switzerland

In memoriam Christian Auer

## INTRODUCTION

The term "guild" describes a group of organisms that exploit the same class of resources in a similar manner (Root 1967, Mattson et al. 1988). This study focuses on six members of the folivore guild of subalpine larch, *Larix decidua*, in Switzerland--five lepidopterans and one hymenopteran. From 1949 to 1979, Auer (1977) sampled populations of the larch bud moth, *Zeiraphera diniana* L., and at the same time collected associated larvae. I have analyzed these 30 years of insect sample data for the six different species and now offer it to the scientific literature. In spite of some methodological shortcomings, the data have tremendous value because of their historical import. There are precious few long-term data sets of this kind.

The spectacular population cycles of the larch bud moth (LBM) and the ensuing periodic severe defoliations of the subalpine larch forests have provided an interesting opportunity to analyze possible interspecific competition among members of the larch folivore guild owing to varying degrees of depletion of their common food source. The impact of defoliation on each member of the guild is evaluated by comparing trends (immediate and delayed) in the population index of each with the larch bud moth (LBM) cycle.

By analogy to what happens to the LBM, "immediate impact" is understood as increased larval mortality and reduced fecundity due to loss of shelter and starvation, whereas "delayed impact" results from the "induced response" which is mediated by the lower food quality in years subsequent to defoliation and results in drastically increased mortality of the small larvae for several succeeding generations. I used Chi-square analysis to compare the trends in fluctuation patterns of the guild members with the LBM. I examine the hypothesis that interspecific competition driven by the LBM contributes to the quantitative structuring of the guild.

## EXPERIMENTAL METHODS

### Biology and Phenology of Guild Members

Although there are many insects associated with the large larval instars of the LBM, only the six most frequent phytophagous species are considered (Fig. 1).

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BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

1) Tortricidae

a) *Exapate duratella* Heyd. is polyphagous on mountain ash (*Sorbus aucuparia*), shrubs (*Vaccinium*, *Rhododendron*, and *Cotoneaster*), or herbs (*Thalictrum*) growing underneath larch (Thomann 1947). It occurs throughout the alpine region and overwinters in the egg stage. Hatching occurs somewhat later than the LBM. It has five larval instars which construct fascicles similar to those of the LBM. Rather agile when disturbed, they descend on silken threads to lower branches or to the ground. If not disturbed, *E. duratella* pupates on larch. The species is sexually dimorphic: males are winged and white; females are wingless and dark gray. Females are very cold-hardy, surviving temperatures as low as -18°C, and are active at air temperatures as low as 5°C (Baltensweiler 1961).

b) *Ptycholomoides aeriferana* H.-Schaeff. is oligophagous on *Acer platanoides*, *Larix*, and pine (Raigorodskaya 1963). Palearctic in distribution, it is found from Europe to Japan. This species hatches from the egg in fall, molts to the second instar without feeding, and overwinters in diapause. It starts to feed in the spring, simultaneous with the LBM. After the fifth larval instar, pupation takes place between the needles. The female attaches her eggs to the needles by means of an adhesive substance. Highest densities usually occur at altitudes below 1700 m.

c) *Spilonota laricana* Hein. is monophagous on larch and palearctic in distribution (Bovey 1978). The eggs are deposited on needles in June to August, depending on altitude. The first instar larvae hatch after 2 weeks and overwinter as second instar larvae in a hibernaculum. Emergence takes place during needle growth of larch. The larvae construct a fascicle similar to that of the LBM. Pupation occurs between needles and the moths emerge after 2 to 3 weeks. Highest densities usually occur at altitudes below 1700 m.

2) Geometridae

*Oporinia (Epirrita) autumnata* Bkh. is polyphagous, living on birch, larch, fir, and spruce. Extensive outbreaks occur on birch in Scandinavia (Tenow 1972). The species being univoltine, eggs are deposited singly on branches, where they overwinter. Hatching occurs in early spring. The five larval instars live openly along the branch axis and feed on needles without spinning a fascicle. Thus the larvae are very easily dislodged when the branch samples are collected if precautions are not taken. Losses of 30 percent and 53 percent were observed when the branch samples were thrown to the ground from the lower and middle to upper crown levels respectively (Bidaud 1970). Pupation occurs on the ground. The moths are not very good flyers.

3) Gelechidae

*Teleia saltuum* Z. is oligophagous and palearctic in distribution. Its biology is not very well known, but the insect seems to occur primarily at low altitudes. It is a biennial species, overwintering both as L2- and L5-larvae. Eggs are deposited on needles.

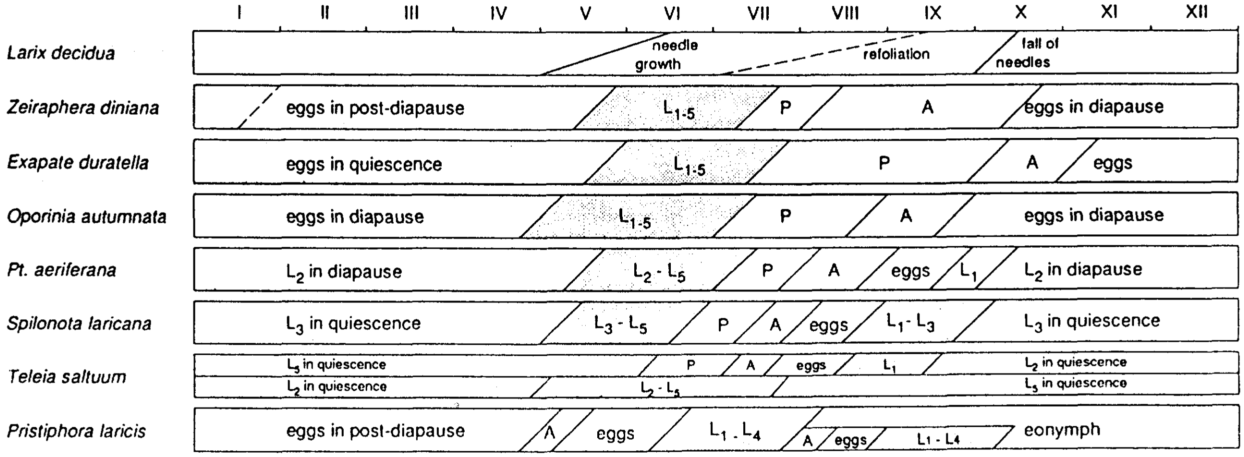

Figure 1. Phenology and biology of the folivore guild on larch (*Larix decidua* Mill.) in the European Alps.

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4) Tenthredinidae

*Pristiphora laricis* Htg. is monophagous and palearctic in its distribution. At lower altitudes two generations occur per year; above 1700 m only a partial second generation is observed. Overwintering as an eonymph in a cocoon, it transforms to a pronymph in January (Lovis 1975), and the adults emerge toward the end of May and beginning of June. Eggs of the first generation are laid on the growing needles and hatch after 10 days at 16°C or 21 days at 10°C.

## Larval Population Sample

The sampling methodology for the LBM and its associated guild members (Kälin and Auer 1954, Auer 1961) relies on a sampling scheme stratified according to topography (altitude and exposure) and host tree density per unit area in the subalpine forest, e.g. *Larici-pinetum-cembrae* (Ellenberg and Klötzli 1972). The proper sample provides a basic population estimate for the larval stage of each generation on a weight basis, i.e. number of larvae per kg of larch twigs with foliage. It is comprised of three branches cut at three levels within the crown of the tree. The samples are taken when the LBM is in its fourth or fifth instar. This coincides phenologically with the time at which the larch needles cease to grow.

Five outbreak areas along the alpine arch, covering 2120 to 6280 ha of montane and subalpine forests, were sampled between 1949 and 1976 with 100 to 500 sample trees for various periods (Auer 1977):

1) the region of the Briançonnais in the western Alps (Department Hautes Alpes, France)
2) the Goms in the Upper Rhone River Valley (Kanton Wallis, Switzerland)
3) the Oberengadin (Kanton Graubünden, Switzerland)
4) the Valle Aurina (Provincia Autonoma di Bolzano-Alto Adige, Italy)
5) the Lungau (Land Salzburg, Austria).

## Evaluation of the Defoliation Impact on the Guild Members

Two negative effects of defoliation on the fluctuations of the guild members are conceivable.

1) An immediate impact. Assuming that the destruction and depletion of the common food resource in the current generation t induces immediate larval mortality due to malnutrition or lack of shelter and reduces, therefore, the egg potential of the following generation, the immediate impact is a lower larval density in generation t+1:

   [If Density $\mathrm{LBM}_t$ > 100 larvae/kg: Density $x_{t+1}$ < Density $x_t$].

   *Pristiphora laricis*, whose first generation larval period coincides exactly with the large larval stages of the LBM, might suffer heavy mortality in the same generation t, and therefore the immediate impact is defined by [Density $\mathrm{Pl}_t$ < Density $\mathrm{Pl}_{t-1}$].

2) A delayed impact. Defoliation of the larch lowers the long-term nutritional quality of the larch needles in subsequent generations, a condition which may relax only over the course of several years (Baltensweiler 1984, Baltensweiler and Fischlin 1988). This impact is defined as follows:

   [If Density $\mathrm{LBM}_t$ > 100 larvae/kg: Density $x_{t+2}$ < Density $x_{t+1}$;
   Density $\mathrm{Pl}_{t+1}$ < Density $\mathrm{Pl}_t$].

   The differences in density are evaluated as trends only, and the occurrence of cases is tested by Chi-square analysis. The error probabilities are given as percentages.

## RESULTS

The densities for the LBM and its associated species on larch in five different subalpine regions are presented in Tables 1 through 7. The fluctuation pattern of the guild as a whole is remarkably similar at all five subalpine sites. In four to five generations, the LBM increases by five orders of magnitude and transgresses the defoliation threshold of 100 larvae/kg twigs at regular intervals of 8 to 9 years (Baltensweiler et al. 1977). Conversely, the numbers of the other guild members vary with a moderate amplitude between 0.01 and 5 larvae/kg twigs, but without exhibiting any particular trend. This is somewhat surprising since one might have assumed that the severe and widespread defoliation by the LBM would synchronize the fluctuations of the other phytophagous species with each other.

Table 1. *Zeiraphera diniana* density (larvae/kg)

| Year | Briançonnais | Goms | Oberengadin | Valle Aurina | Lungau |
|---|---|---|---|---|---|
| 1952 | | | 4.174 | | |
| 1953 | | | 68.797 | | |
| 1954 | | | 331.760 | | |
| 1955 | | | 126.541 | | |
| 1956 | | | 21.280 | | |
| 1957 | | | 2.246 | | |
| 1958 | | 0.049 | 0.085 | | |
| 1959 | | 0.090 | 0.080 | | |
| 1960 | 4.422 | 0.458 | 0.371 | 0.040 | |
| 1961 | 48.303 | 1.774 | 1.638 | 0.140 | 0.090 |
| 1962 | 361.879 | 10.902 | 22.878 | 2.420 | 0.560 |
| 1963 | 53.440 | 151.132 | 248.817 | 39.260 | 8.760 |
| 1964 | 70.770 | 175.215 | 184.272 | 180.460 | 107.870 |
| 1965 | 0.475 | 3.235 | 3.116 | 21.880 | 234.576 |
| 1966 | 0.024 | 0.013 | 0.020 | 0.280 | 38.540 |
| 1967 | 0.041 | 0.025 | 0.002 | 0.020 | 0.290 |
| 1968 | 0.335 | 0.025 | 0.059 | 0.050 | 0.040 |
| 1969 | 2.152 | 0.180 | 0.197 | 0.150 | 0.183 |
| 1970 | 10.114 | 1.495 | 1.068 | 0.752 | 0.707 |
| 1971 | 81.913 | 10.338 | 10.569 | 3.810 | 3.170 |
| 1972 | 245.787 | 76.355 | 173.932 | 8.330 | 29.820 |
| 1973 | 1.371 | 78.225 | 249.612 | 4.255 | 36.060 |
| 1974 | 0.396 | 8.075 | 176.050 | 4.029 | 118.450 |
| 1975 | 0.258 | 0.190 | 4.749 | 4.740 | 18.380 |
| 1976 | 0.618 | 0.050 | 0.014 | 0.441 | 3.760 |
| 1977 | 3.600 | | 0.008 | 0.118 | 0.830 |
| 1978 | 36.144 | 0.600 | 0.056 | 0.068 | 0.240 |
| 1979 | 209.531 | 1.616 | 0.204 | 0.130 | 0.170 |

Table 2. *Exapate duratella* density (larvae/kg)

| Year | Briançonnais | Goms | Oberengadin | Valle Aurina | Lungau |
|---|---|---|---|---|---|
| 1952 | | | 0.018 | | |
| 1953 | | | 0.282 | | |
| 1954 | | | 0.826 | | |
| 1955 | | | 0.134 | | |
| 1956 | | | 0.018 | | |
| 1957 | | | 0.002 | | |
| 1958 | | 0.012 | 0.004 | | |
| 1959 | | 0.050 | 0.070 | | |
| 1960 | 1.402 | 0.497 | 0.220 | 0.090 | |
| 1961 | 2.945 | 0.241 | 0.166 | 0.100 | 0.040 |
| 1962 | 5.556 | 0.451 | 1.228 | 0.160 | 0.090 |
| 1963 | 3.500 | 1.130 | 5.573 | 0.490 | 0.250 |
| 1964 | 0.330 | 0.960 | 2.830 | 0.280 | 0.200 |
| 1965 | 0.030 | 0.207 | 0.388 | 0.170 | 0.212 |
| 1966 | 0.008 | 0.010 | 0.011 | 0.010 | 0.140 |
| 1967 | 0.055 | 0.010 | 0.022 | 0.010 | 0.050 |
| 1968 | 0.413 | 0.050 | 0.034 | 0.070 | 0.050 |
| 1969 | 0.432 | 0.170 | 0.099 | 0.020 | 0.069 |
| 1970 | 0.530 | 0.325 | 0.619 | 0.163 | 0.100 |
| 1971 | 1.258 | 0.798 | 1.411 | 0.310 | 0.310 |
| 1972 | 1.179 | 0.615 | 6.833 | 0.220 | 0.150 |
| 1973 | 0.210 | 2.145 | 2.844 | 0.118 | 0.190 |
| 1974 | 0.028 | 0.530 | 0.798 | 0.128 | 0.100 |
| 1975 | 0.220 | 0.060 | 0.042 | 0.110 | 0.090 |
| 1976 | 0.542 | 0.045 | 0.008 | 0.039 | 0.110 |
| 1977 | 1.360 | | 0.010 | 0.176 | 0.080 |
| 1978 | 1.288 | 0.040 | 0.015 | 0.078 | 0.010 |
| 1979 | 6.133 | 0.101 | 0.050 | 0.010 | 0.050 |

Table 3. *Oporinia autumnata* density (larvae/kg)

| Year | Briançonnais | Goms | Oberengadin | Valle Aurina | Lungau |
|---|---|---|---|---|---|
| 1952 | | | 0.287 | | |
| 1953 | | | 0.669 | | |
| 1954 | | | 0.994 | | |
| 1956 | | | 0.202 | | |
| 1957 | | | 0.106 | | |
| 1958 | | | 0.134 | | |
| 1958 | | 0.531 | 0.361 | | |
| 1959 | | 0.668 | 0.838 | | |
| 1960 | 1.074 | 1.047 | 0.707 | 0.960 | |
| 1961 | 0.780 | 0.670 | 0.417 | 0.310 | 0.530 |
| 1962 | 0.414 | 3.284 | 2.185 | 0.930 | 0.850 |
| 1963 | 0.560 | 6.320 | 2.354 | 1.260 | 0.900 |
| 1964 | 0.600 | 10.388 | 0.850 | 0.980 | 1.650 |
| 1965 | 0.530 | 2.530 | 0.286 | 0.40 | 1.151 |
| 1966 | 0.412 | 0.328 | 0.124 | 0.330 | 0.610 |
| 1967 | 2.950 | 0.450 | 0.248 | 0.490 | 0.420 |
| 1968 | 4.883 | 1.445 | 0.888 | 1.385 | 0.580 |
| 1969 | 2.472 | 2.205 | 1.063 | 2.730 | 0.752 |
| 1970 | 0.225 | 1.795 | 0.788 | 1.693 | 1.153 |
| 1971 | 0.255 | 1.581 | 1.047 | 1.360 | 1.360 |
| 1972 | 0.168 | 1.085 | 0.912 | 0.290 | 1.370 |
| 1973 | 0.196 | 0.990 | 0.572 | 0.216 | 0.440 |
| 1974 | 0.458 | 3.035 | 0.508 | 0.676 | 1.040 |
| 1975 | 0.740 | 1.060 | 0.128 | 0.880 | 0.570 |
| 1976 | 0.570 | 0.550 | 0.361 | 0.667 | 0.590 |
| 1977 | 3.760 | | 0.229 | 2.197 | 0.590 |
| 1978 | 18.394 | 1.590 | 0.696 | 1.255 | 0.690 |
| 1979 | 5.449 | 0.909 | 0.240 | 0.485 | 0.240 |

Table 4. *Ptycholomoides aeriferana* density (larvae/kg)

| Year | Briançonnais | Goms | Oberengadin | Valle Aurina | Lungau |
|---|---|---|---|---|---|
| 1952 | | | 0.001 | | |
| 1953 | | | 0.018 | | |
| 1954 | | | 0.006 | | |
| 1955 | | | 0.002 | | |
| 1956 | | | 0.001 | | |
| 1957 | | | 0.001 | | |
| 1958 | | 0.001 | 0.002 | | |
| 1959 | | 0.001 | 0.002 | | |
| 1960 | 0.225 | 0.007 | 0.002 | 0.010 | |
| 1961 | 0.037 | 0.001 | 0.002 | 0.010 | 0.010 |
| 1962 | 0.667 | 0.113 | 0.026 | 0.070 | 0.020 |
| 1963 | 0.160 | 0.085 | 0.032 | 0.250 | 0.010 |
| 1964 | 0.090 | 0.093 | 0.016 | 0.210 | 0.560 |
| 1965 | 0.010 | 0.010 | 0.016 | 0.110 | 0.101 |
| 1966 | 0.004 | 0.003 | 0.002 | 0.060 | 0.160 |
| 1967 | 0.005 | 0.005 | 0.002 | 0.010 | 0.030 |
| 1968 | 0.065 | 0.005 | 0.002 | 0.095 | 0.020 |
| 1969 | 0.221 | 0.010 | 0.007 | 0.115 | 0.064 |
| 1970 | 0.040 | 0.085 | 0.007 | 0.118 | 0.127 |
| 1971 | 0.240 | 0.061 | 0.053 | 0.310 | 0.310 |
| 1972 | 0.026 | 0.050 | 0.019 | 0.070 | 0.070 |
| 1973 | 0.019 | 0.220 | 0.012 | 0.029 | 0.110 |
| 1974 | 0.028 | 0.055 | 0.006 | 0.098 | 0.020 |
| 1975 | 0.001 | 0.010 | 0.002 | 0.070 | 0.140 |
| 1976 | 0.092 | 0.040 | 0.002 | 0.069 | 0.110 |
| 1977 | 0.150 | | 0.002 | 0.088 | 0.080 |
| 1978 | 0.356 | 0.040 | 0.002 | 0.010 | 0.050 |
| 1979 | 0.327 | 0.010 | 0.002 | 0.010 | 0.010 |

Table 5. *Spilonota laricana* density (larvae/kg)

| Year | Briançonnais | Goms | Oberengadin | Valle Aurina | Lungau |
|---|---|---|---|---|---|
| 1952 | | | 0.031 | | |
| 1953 | | | 0.065 | | |
| 1954 | | | 0.125 | | |
| 1955 | | | 0.103 | | |
| 1956 | | | 0.017 | | |
| 1957 | | | 0.009 | | |
| 1958 | | 0.142 | 0.026 | | |
| 1959 | | 0.150 | 0.022 | | |
| 1960 | 0.451 | 0.593 | 0.043 | 0.070 | |
| 1961 | 0.404 | 0.084 | 0.027 | 0.070 | 0.010 |
| 1962 | 0.273 | 0.255 | 0.039 | 0.060 | 0.007 |
| 1963 | 0.400 | 0.220 | 0.043 | 0.190 | 0.270 |
| 1964 | 0.180 | 0.113 | 0.138 | 0.220 | 0.110 |
| 1965 | 0.265 | 0.397 | 0.174 | 0.430 | 0.889 |
| 1966 | 0.092 | 0.065 | 0.041 | 0.120 | 0.550 |
| 1967 | 0.486 | 0.160 | 0.029 | 0.110 | 0.250 |
| 1968 | 1.644 | 0.175 | 0.086 | 0.160 | 0.220 |
| 1969 | 0.085 | 0.295 | 0.091 | 0.145 | 0.173 |
| 1970 | 0.115 | 0.275 | 0.035 | 0.118 | 0.060 |
| 1971 | 0.828 | 0.121 | 0.070 | 0.450 | 0.450 |
| 1972 | 0.124 | 0.060 | 0.101 | 0.200 | 0.470 |
| 1973 | 0.201 | 0.110 | 0.151 | 0.157 | 0.160 |
| 1974 | 0.134 | 0.210 | 0.136 | 0.382 | 0.810 |
| 1975 | 0.150 | 0.040 | 0.155 | 0.270 | 0.290 |
| 1976 | 0.127 | 0.105 | 0.084 | 0.539 | 0.290 |
| 1977 | 0.230 | | 0.049 | 0.127 | 0.100 |
| 1978 | 0.182 | 0.130 | 0.022 | 0.088 | 0.110 |
| 1979 | 0.163 | 0.061 | 0.030 | 0.019 | 0.030 |

Table 6. *Teleia saltuum* density (larvae/kg)

| Year | Briançonnais | Goms | Oberengadin | Valle Aurina | Lungau |
|---|---|---|---|---|---|
| 1952 | | | 0.297 | | |
| 1953 | | | 0.166 | | |
| 1954 | | | 0.162 | | |
| 1955 | | | 0.033 | | |
| 1956 | | | 0.024 | | |
| 1957 | | | 0.042 | | |
| 1958 | | 0.234 | 0.018 | | |
| 1959 | | 0.185 | 0.112 | | |
| 1960 | 0.338 | 0.500 | 0.056 | 0.580 | |
| 1961 | 0.321 | 0.240 | 0.040 | 1.310 | 0.430 |
| 1962 | 0.111 | 0.363 | 0.125 | 0.590 | 0.280 |
| 1963 | 0.130 | 0.360 | 0.061 | 3.050 | 1.450 |
| 1964 | 0.030 | 0.080 | 0.028 | 0.110 | 0.210 |
| 1965 | 0.040 | 0.105 | 0.073 | 1.210 | 1.354 |
| 1966 | 0.028 | 0.143 | 0.026 | 0.180 | 0.270 |
| 1967 | 0.202 | 0.130 | 0.046 | 0.210 | 0.950 |
| 1968 | 0.680 | 0.100 | 0.038 | 0.420 | 0.310 |
| 1969 | 0.452 | 0.215 | 0.113 | 0.940 | 0.391 |
| 1970 | 0.065 | 0.325 | 0.060 | 0.497 | 0.313 |
| 1971 | 0.169 | 0.197 | 0.034 | 2.340 | 2.340 |
| 1972 | 0.051 | 0.050 | 0.068 | 1.950 | 1.200 |
| 1973 | 0.024 | 0.030 | 0.006 | 0.206 | 0.230 |
| 1974 | 0.013 | 0.060 | 0.010 | 2.274 | 1.140 |
| 1975 | 0.040 | 0.010 | 0.013 | 0.410 | 0.190 |
| 1976 | 0.077 | 0.010 | 0.008 | 0.559 | 0.970 |
| 1977 | 0.080 | | 0.006 | 0.608 | 0.670 |
| 1978 | 0.058 | 0.040 | 0.007 | 0.225 | 0.850 |
| 1979 | 0.041 | 0.020 | 0.220 | 0.010 | 0.220 |

Table 7. *Pristiphora laricis* density (larvae/kg)

| Year | Briançonnais | Goms | Oberengadin | Valle Aurina | Lungau |
|---|---|---|---|---|---|
| 1952 | | | 0.181 | | |
| 1953 | | | 0.198 | | |
| 1954 | | | 0.352 | | |
| 1955 | | | 0.084 | | |
| 1956 | | | 0.225 | | |
| 1957 | | | 0.887 | | |
| 1958 | | 1.901 | 2.587 | | |
| 1959 | | 1.345 | 2.657 | | |
| 1960 | 0.525 | 2.500 | 1.986 | 4.500 | |
| 1961 | 0.514 | 0.394 | 0.949 | 1.920 | 2.340 |
| 1962 | 0.929 | 1.402 | 2.284 | 1.880 | 5.010 |
| 1963 | 0.360 | 0.400 | 0.939 | 1.450 | 3.730 |
| 1964 | 0.730 | 0.345 | 0.262 | 1.130 | 2.080 |
| 1965 | 1.820 | 0.667 | 1.000 | 1.160 | 0.545 |
| 1966 | 2.936 | 0.642 | 1.872 | 0.850 | 0.880 |
| 1967 | 1.694 | 2.115 | 2.477 | 2.550 | 0.610 |
| 1968 | 1.952 | 3.620 | 3.551 | 2.985 | 0.970 |
| 1969 | 1.422 | 1.720 | 1.753 | 2.195 | 1.278 |
| 1970 | 1.805 | 1.815 | 3.198 | 3.431 | 3.740 |
| 1971 | 0.562 | 1.263 | 2.787 | 1.430 | 1.430 |
| 1972 | 0.336 | 1.335 | 3.001 | 1.170 | 1.840 |
| 1973 | 0.708 | 2.125 | 0.739 | 0.961 | 1.080 |
| 1974 | 0.239 | 2.090 | 0.322 | 3.010 | 1.000 |
| 1975 | 4.350 | 1.710 | 1.292 | 2.570 | 0.530 |
| 1976 | 16.585 | 4.790 | 0.247 | 4.382 | 0.790 |
| 1977 | 1.730 | | 3.465 | 1.912 | 2.110 |
| 1978 | 1.404 | 1.050 | 1.988 | 1.156 | 1.880 |
| 1979 | 2.878 | 1.283 | 1.780 | 1.942 | 1.780 |

Table 8. Significance tests ($Chi^2$, error probabilities in %) of the immediate or the delayed impact due to defoliation of the larch by the LBM on the fluctuations of the guild members (for further explanation see text).

| | Immediate response | | | Delayed response | | |
|---|---|---|---|---|---|---|
| | Yes | No | %p | Yes | No | %p |
| *Exapate duratella* | 13 | 2 | 0.45 | 14 | 1 | 0.08 |
| *Oporinia autumnata* | 11 | 4 | 7.07 | 9 | 6 | 43.86 |
| *Pt. aeriferana* | 10 | 5 | 19.67 | 10 | 5 | 19.67 |
| *Spilonota laricana* | 5 | 10 | 19.67 | 10 | 5 | 19.67 |
| *Teleia saltuum* | 8 | 7 | 79.63 | 8 | 7 | 79.63 |
| *Pristiphora laricis* | 11 | 4 | 7.07 | 8 | 7 | 79.63 |

By examining possible immediate and delayed effects of defoliation on the fluctuation patterns of the individual species, one obtains a more revealing insight (Table 8). For ease of interpretation, the fluctuation patterns of the six species are compared to the LBM cycle in the Oberengadin (*Z. diniana*: mean density 58.31 larvae/kg; coefficient of variation (CV) 167 percent), as shown in Figs. 2a and 2b.

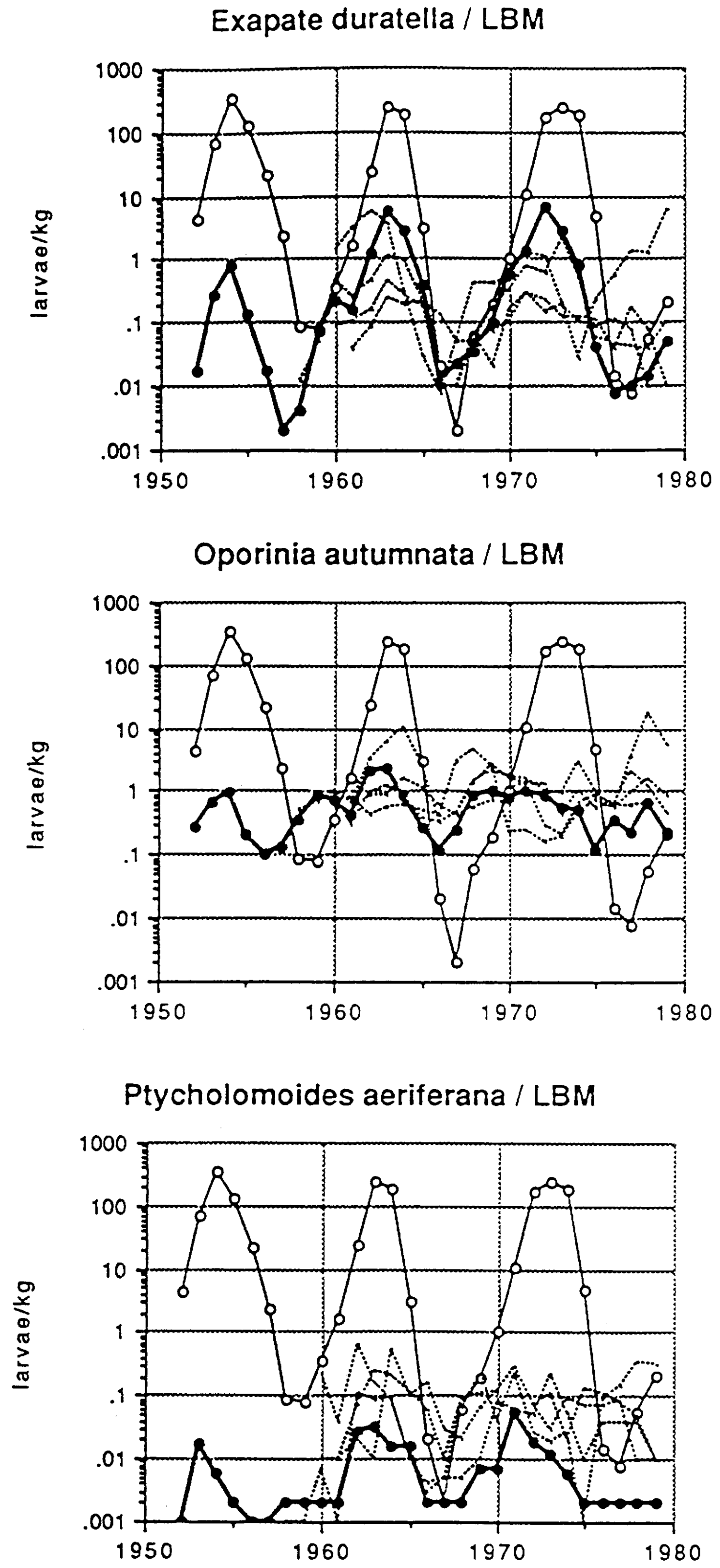
1) *Exapate duratella.* Mean density 0.88 larvae/kg. Exhibits a cycle synchronous to the LBM and of large amplitude (CV 194 percent). The hypothesis of a significant immediate impact is accepted ($p < 0.01$), but there is also a highly significant delayed impact ($p < 0.10$). In two of the three cycles, *E. duratella* exhibits the highest densities of all associated species.

2) *Oporinia autumnata.* Mean density 0.65 larvae/kg; CV 85 percent. In all three LBM cycles, the immediate impact is apparent, but there are three more minor peaks asynchronous with the LBM maxima. This suggests that processes other than the interspecific impact of the LBM (immediate impact: $p = 0.07$), but of similar efficiency, regulate the densities of *O. autumnata.* In the Briançonnais, maximal densities of *O. autumnata* are observed when LBM densities range from 0.3 to 36 larvae/kg.

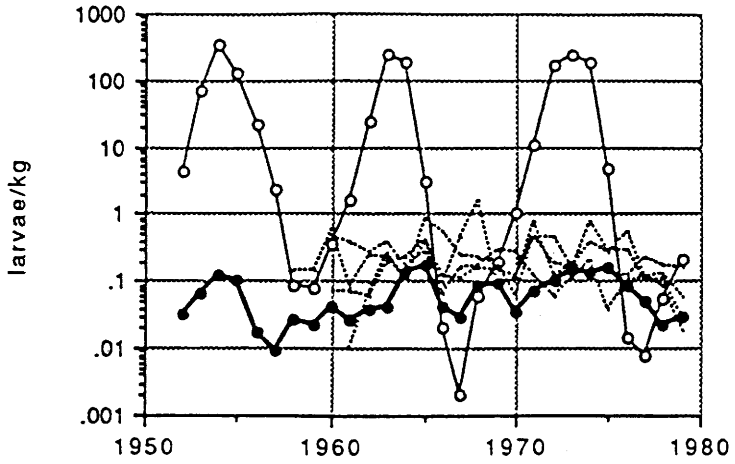
3) *Ptycholomoides aeriferana.* Mean density 0.009 larvae/kg; CV 136 percent. The fluctuation of the Engadine population suggests coincidence with the LBM cycle, but because in 15 out of 28 years no larvae were recorded, no further comment is made.

4) *Spilonota laricana.* Mean density 0.07 larvae/kg; CV 70 percent. The species fluctuates at a minor amplitude, so the hypothesis of an immediate impact has to be rejected ($p = 0.20$), whereas the hypothesis of a delayed impact shows an error probability of only 0.07, inclining one toward acceptance.

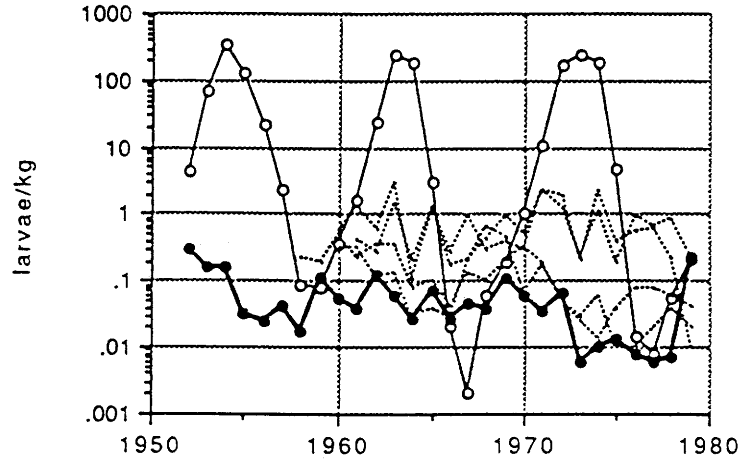
5) *Teleia saltuum.* Mean density 0.07 larvae/kg; CV 105 percent. Population increases and decreases alternate rapidly and independently of the LBM densities, so both impact hypotheses have to be rejected ($p = 0.80$).



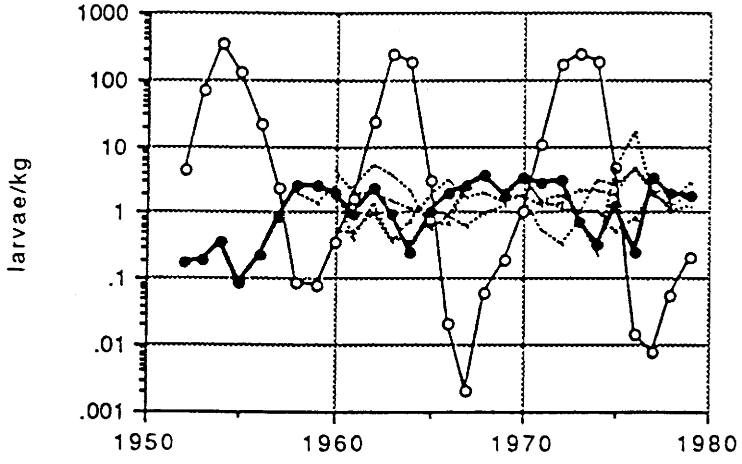
Figures 2a. Fluctuation patterns of guild members on larch from five subalpine regions in the European Alps (•••••) compared with the fluctuations of the larch bud moth (LBM) (o———o) and the relevant species (•▬▬•) in the Oberengadin from 1952 to 1979. Sampling unit: larvae/kg larch twigs.



Spilonota laricana / LBM



Teleia saltuum / LBM



Pristiphora laricis / LBM

Figures 2b. Fluctuation patterns of guild members on larch from five subalpine regions in the European Alps (•••••) compared with the fluctuations of the larch bud moth (LBM) (o——o) and the relevant species (●━━●) in the Oberengadin from 1952 to 1979. Sampling unit: larvae/kg larch twigs.

6) *Pristiphora laricis*. Mean density 1.54 larvae/kg; CV 73 percent. The fluctuation of Pl in the Engadine (Fig. 2b) suggests that an immediate impact is exerted by the LBM, i.e. the density of Pl is reduced already during the year of defoliation from that of the previous generation. This tendency is confirmed when all the data from the alpine arch ($p = 0.07$) are considered, whereas the hypothesis of a delayed impact is a chance event ($p = 0.80$).

## CONCLUSIONS

Analysis of an immediate and a delayed interspecific impact of defoliation of the larch by the LBM on the fluctuation of six guild members reveals that out of 12 possible cases only the two related to *E. duratella* are significant ($p < 0.01$), and two more cases show a mere "close to significant" probability. In spite of methodological constraints, such as the evaluation of densities related to the biology of the LBM and not related to the individual species, or the grossly generalized assumption of the near to complete defoliation of larch forests over large areas, this result is surprising. Although comparison of the fluctuation curves clearly shows a parallel negative population trend (with the possible exception of *T. saltuum*), the nonsignificance is due to the asynchrony in population trends with the cycle of the LBM. This asynchrony is caused by the fluctuations at much lower densities which result in smaller amplitudes. Maximal densities of *Oporinia*, *Ptycholomoides*, *Spilonota*, and *Pristiphora*, which correlate with minimal densities of the LBM or densities well below defoliation threshold, suggest that these guild members are not regulated by interaction with the food quality. This conclusion was confirmed on two occasions when the LBM failed to transgress the defoliation threshold--in the Valle Aurina in 1973 and 1975 (Fig. 3) and Goms in 1972--but the guild members did not deviate from their general pattern of fluctuation. Furthermore, it is interesting to note that, with the exception of *Exapate*, trends indicating an interspecific impact (*Oporinia* and *Pristiphora*) are related to the immediate impact, i.e. to the lack of food and loss of shelter, but not to the delayed impact due to reduced food quality.

Clearly, the folivore guild feeding on larch trees may be classified into two groups: those species which respond to the self-induced change in food quality by a drastic decline in population (LBM and *Exapate*); and those species which lack such a specific response (*Oporinia*, *Ptycholomoides*, *Spilonota*, *Teleia*, and *Pristiphora*). This finding is next discussed as a function of the plant carbon/nutrient balance (Bryant et al. 1988, Tuomi et al. 1988).

### Aspects Relevant to the Host Plant

A pioneer species, *Larix decidua* has evolved in harsh climates and environments of low productivity which make for inherently slow growth and are thought to favor the evolution of constitutive antiherbivore defenses (Bryant et al. 1988). Unfortunately, allelochemicals have not yet been investigated in larch needles, but several other criteria serving as food value indices, such as growth rate (Baltensweiler 1984, 1985) and nitrogen and fiber concentrations (Benz 1974, Omlin and Herren 1976), are known to be strongly correlated with growth responses of the larch to abiotic or biotic constraints. As water consumption, photosynthetic capacity, and nitrogen concentrations are positively correlated with each other, the growth rate of needles responds immediately to the prevailing weather conditions. Consequently, growth conditions and nitrogen concentrations are reflected in an integrated manner by the shape of the growth curve and the final length of the needles (Fig. 4). Much more drastic effects on the physiology of the tree are to be expected from defoliation. Late frosts in spring may kill the new needle biomass and necessitate refoliation, whereas early frosts in fall may destroy needles and prevent the resorption of nutrients into the stem. In either case the flush of needles in the following spring remains short and stiff. Precisely the same effects are observed after artificial and/or natural defoliation by the LBM (Benz 1974, Omlin 1980, Baltensweiler 1985). The reduced food value of such needles for lepidopteran larvae is due not only to the physical properties of the needles, but also to their reduced nitrogen content (Benz 1974, Fischlin and Baltensweiler 1979, Omlin 1980). These effects are all in agreement with the predictions derived from the model of plant carbon/nutrient balance (Tuomi et al. 1988).

## Aspects Relevant to the Insects

LBM and *E. duratella* display the highest mean densities in the subalpine forests. They both show developmental and behavioral adaptations to low temperatures--LBM in the egg stage (Bakke 1969) and *E. duratella* in oviposition (Baltensweiler 1961)--which enables them to cope successfully with the harsh subalpine environment. But even more relevant in this context are characteristics such as the early hatching, and the feeding of the first two instars close to meristematic plant tissue, which reflects their adaptations to exploit one of the most nitrogen-rich food resources in the subalpine environment (Baltensweiler in prep.).

In contrast to LBM and *E. duratella*, the four guild members *Ptycholomoides*, *Spilonota*, *Teleia*, and *Pristiphora* show highest mean densities on larch near Zürich at 600 m a.s.l. (Auer, unpubl.). *Spilonota*, *Teleia*, and *Pristiphora* are "late season species" (Fig. 1), which means in general that they are obliged to be much more tolerant of low food quality, considering the usual maturational decline in foliar nutrients (Clancy et al. 1988). It is thus not at all surprising that reduced nutritional quality of larch foliage due to LBM defoliation does not constrain the population dynamics of these guild members appreciably. In accord with this conclusion is the finding that the trends in interspecific impact due to LBM defoliation (*Oporinia* and *Pristiphora*) are due more to the immediate impact, which is mainly quantitative lack of food and loss of shelter, and not to the delayed impact, which consists of reduced food quality. These findings, then, allow us to conclude that the trophic interrelation between larch and the two food specialists LBM and *E. duratella* may be interpreted as an adaptation of the insects to the physiologic responses of the larch to its abiotic environment. Thus the hypothesis of a quantitative defense reaction of the larch tree to the impact of specialistic herbivores would violate rules of parsimony.

No specific and detailed studies have been made to determine the processes which might regulate the various guild members on larch in the subalpine region. Information on the fecundity of subalpine populations is scarce (e.g. *P. aeriferana* 51.8 ± 5.08 eggs/female, n = 6). Polyphagy and voltinism would be important mechanisms to buffer the various species against negative impact by the LBM. Parasitism of the guild members has been investigated in order to evaluate their possible role as alternative hosts to *Z. diniana* (DeLucchi et al. 1974, Lovis 1975). Eighty-one species of parasitoids have been obtained from eggs, larvae, and pupae of the associated species. Twenty-nine of these species also parasitize the LBM, but at a very insignificant rate. One hundred and nine species of primary and secondary parasitoids are known from LBM in the European Alps. However, since its 10 most important parasitoids are monophagous, they cannot exert any direct regulative influence on the population dynamics of the guild members (DeLucchi 1982).

We may conclude that five of the six most important species belonging to the folivore guild on *Larix decidua* exhibit population dynamics remarkably independent from the apparently dominant fluctuation cycle of the LBM. These five species have evolved as trophic generalists, whereas the LBM and *E. duratella* have apparently specialized to exploit the most nutritive niche available. Given the longevity of the larch, defoliation by the LBM does not have an excessively detrimental effect on the population dynamics of its host plant. On the contrary, it could be argued that the larch and the biocoenose would on the whole profit from the faster recycling of the needle biomass and its nutrients. This argument needs to be considered by those who would contend that the physiologic reaction of the larch to defoliation is a defensive reaction to folivores which may have evolved through coevolutionary steps.

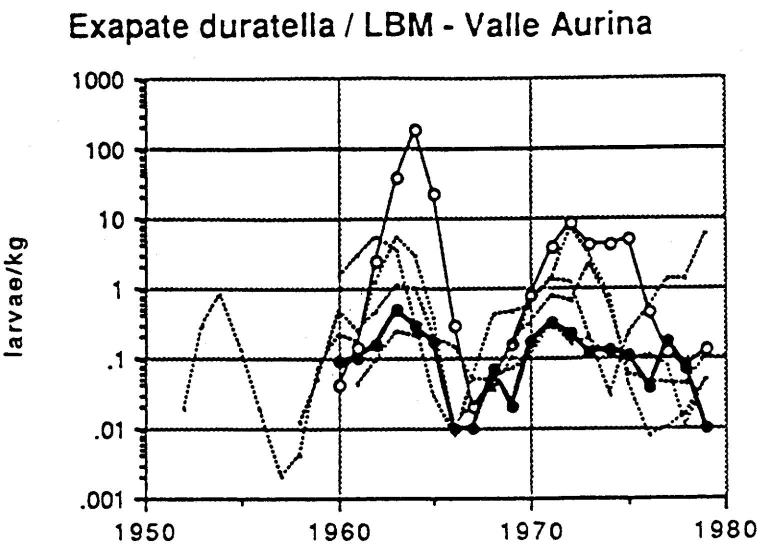


Figure 3. Comparisons of the fluctuation patterns of *Exapate duratella* and the larch bud moth (LBM) in the Valle Aurina (legend as in Figs. 2a and 2b).

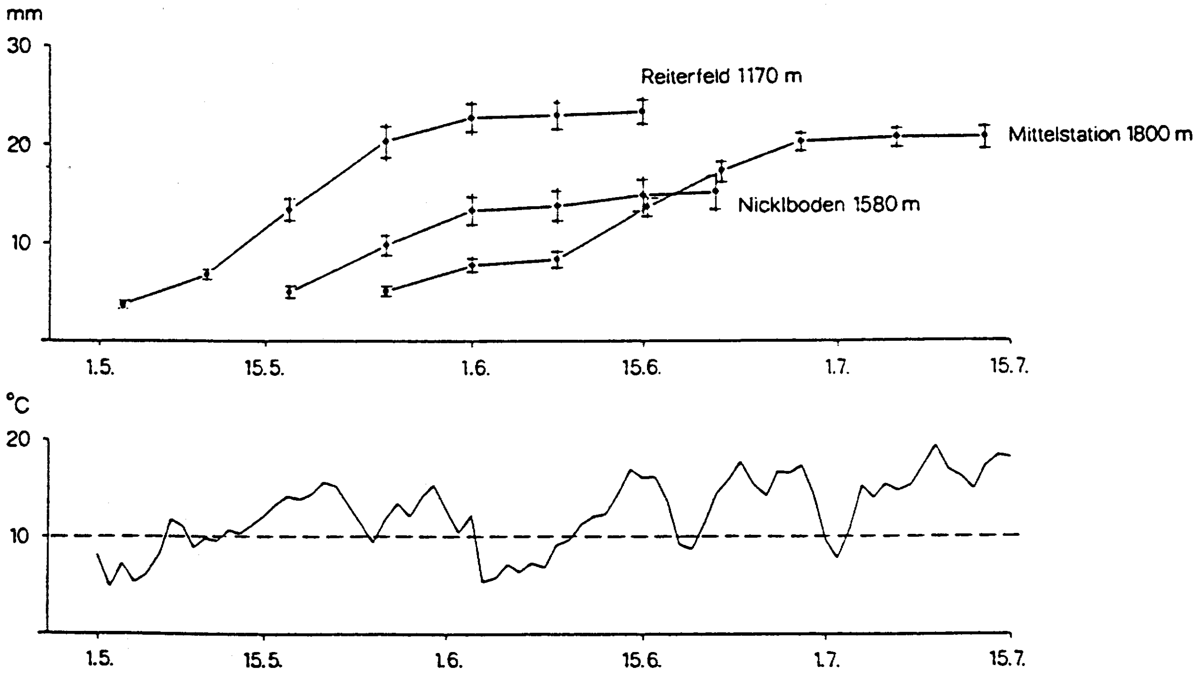


Figure 4. Growth curves of larch needles (mm: x ± $s_x$) in the Lungau at three altitudes in 1975 compared with the daily mean temperature (station Tamsweg, 1021 m a.s.l., °C, min + max/2).

## SUMMARY

Population data obtained from a larval census of the larch bud moth, *Zeiraphera diniana*, and six associated insects feeding on larch needles are presented for five subalpine regions in the European Alps. The fluctuations of these folivore guild members are analyzed vis-a-vis their response to the spectacular periodic defoliation of the larch forests by the larch bud moth. The tortricid species *E. duratella* suffers from a significant impact and exhibits, therefore, a cyclic fluctuation similar to that of the larch bud moth, whereas the other five guild members show a remarkable independence in their fluctuations. It is concluded that their population dynamics in the subalpine zone are not regulated by the variability of the trophic resource, but by different processes. The relationship between the folivore guild and the larch is considered in an evolutionary context.

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