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The Effects of Host Alternation on the Development of Spongy Moth (*Lymantria dispar* L.)

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Abstract

The spongy moth is a significant Lepidopteran species across Europe, where it occurs in oak stands. Tree species composition has a crucial effect on larval development, population density, and outbreaks. Host switching is more likely to occur in a mixed forest than in a monospecific forest. We aimed to better understand the effect of host alternation on the development of the spongy moth. In a laboratory, we reared spongy moth larvae on either (a) Turkey oak (*Quercus cerris* L.) or (b) European hornbeam (*Carpinus betulus* L.) only or on host plants that were changed from Turkey oak to European hornbeam (c) in the early (L_3) or (d) late (L_5) larval instar. Both *Q. cerris* and *C. betulus* proved suitable hosts for the spongy moth larvae. However, the larvae fed exclusively on Turkey oak leaves had better developmental indicators than the others. The groups that switched hosts had weaker developmental indicators than the larvae fed only on Turkey oak but showed better development than the group reared only on Hornbeam leaves. The results of our laboratory research on host switching may offer valuable insights into the developmental dynamics of spongy moths in monospecific forests versus those with higher biodiversity.

Keywords: larval development; outbreak; mortality; host plant switch; nutritional indices; gypsy moth

1. Introduction

The spongy moth (*Lymantria dispar* L.) is a notorious leaf-feeding insect in Central Europe due to its wide distribution and the significant damage it causes. Periodic mass outbreaks are common and result in heavy defoliation across large areas [1–5]. Although it is a polyphagous species with several hundred known host plants worldwide, some plant species are less favorable for larval development. Its primary hosts, such as Pedunculate oak *(Quercus robur* L.), Turkey oak (*Quercus cerris* L.), and hybrid poplars (*Populus* × *euramericana*), promote mass outbreaks of spongy moth in various ways [6]. Host plant metabolites determine larval development, pupation, and hatching and influence reproduction. The chemical contents of host plant leaves also affect the fecundity of the spongy moth and its population dynamics [7]. Continuous and less fragmented assemblages of primary host plants enhance the spread and population growth of the spongy moth [8]. In contrast, a mixed forest with a more diverse composition of tree species, including those that are less suitable hosts for the spongy moth, can be more resilient and better able to compensate for the negative effects of defoliation than monoculture forests dominated by a single primary host plant [9,10]. Such an environment also

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provides improved conditions for a natural enemy complex [5]. Spongy moth larvae thrive on their preferred host plants. When food becomes scarce and their primary host plant is depleted, larvae are more likely to switch to alternative host plants in mixed forests than in monocultures, where the preferred host plant is more abundant. We aimed to assess the effect of host alternation on the development of the spongy moth.

1.1. Host Plant Preference and Suitability Ranking of the Spongy Moth

Host plants are classified into three groups based on their suitability for spongy moth larval development [11]: (1) The first group consists of host plants that support mass multiplication of the larvae with low mortality rates. These tree species include Pedunculate oak (*Quercus robur* L.), Turkey oak (*Quercus cerris* L.), Common alder (*Alnus glutinosa* L.), Common hornbeam (*Carpinus betulus* L.), and hybrid Black poplar clones (*Populus nigra* L.). (2) The second group comprises host trees on which spongy moth larvae can fully develop but no complete defoliation or mass multiplication are observed. Lime (*Tilia* spp.) and Elm species (*Ulmus* spp.), Beech (*Fagus sylvatica* L.), Sessile oak (*Quercus petraea* Liebl.), Black locust (*Robinia pseudoacacia* L.), Scots pine (*Pinus sylvestris* L.), White poplar (*Populus alba* L.), and Balsam poplar species (*Populus* sect. Tacamahaca) belong to this group, as do some shrubs, including Hazel (*Corylus* spp.), Hawthorn (*Crataegus* spp.), Cornel (*Cornus* spp.), and Rose (*Rosa* spp.) species. (3) The third group includes species that spongy moth larvae do not consume at all, such as the European wild pear (*Pyrus pyraster* Burgsdorf), Common privet (*Ligustrum vulgare* L.), Yew (*Taxus baccata* L.), Tree of heaven (*Ailanthus altissima* Swingle), Black elder (*Sambucus nigra* L.), and Spindle species (*Euonymus* spp.).

Other studies have classified host plants according to their nutritional value for spongy moth larvae into four categories [12]. (1) The first category includes host plants that are highly preferred by the larvae, like Oaks (*Quercus* spp.), hybrid Poplars (*Populus* x *euamericana*), Beeches (*Fagus* spp.), Hazels (*Corylus* spp.), Alders (*Alnus* spp.), Mulberries (*Morus* spp.), and Larches (*Larix* spp.). (2) The second category consists of species that offer suitable nutrition in the late larval stages only, which are Hemlocks (*Tsuga* spp.), Pines (*Pinus* spp.), Spruces (*Picea* spp.), and Chestnuts (*Castanea* spp.). (3) The third group includes species that are not preferred by the spongy moth but on which they can still fully develop. These species are Bird cherry (*Padus avium* L.), Easter cottonwood (*Populus deltoides* W. Bartram ex Marshall), Silver maple (*Acer saccharinum* L.), Norway maple (*Acer platanoides* L.), American hornbeam (*Carpinus caroliniana* Walter), and some Elm species (*Ulmus* spp.). (4) Finally, the fourth group consists of species that do not provide suitable nutrition for the spongy moth at all, such as Common hackberry (*Celtis occidentalis* L.).

In addition to the host plants listed above, spongy moth caterpillars consume leaves of various other trees, shrubs, and herbaceous plants, including Apples (*Malus* spp.), Plums (*Prunus* spp.), Lettuce (*Lactuca sativa* L.), Potato (*Solanum tuberosum* L.), Cherry laurel (*Prunus* sect. *Laurocerasus* Benth. and Hook. f.), and Rhododendrons (*Rhododendron* spp.), to various degrees. The caterpillar does not eat Lilac *(Syringa vulgaris* L.) at all [13].

Further studies examined defoliation caused by the spongy moth in various host plant species. According to these articles, spongy moth larvae often feed on Norway spruce (*Picea abies* (L.) H. Karst), Blue spruce (*Picea pungens* Engelm), European larch (*Larix decidua* Miller), Blackthorn (*Prunus spinosa* L.), and Beech (*Fagus slyvatica* L.) [4,14–17]. Among fruit trees, the moth causes serious damage to Plums (*Prunus* spp.) and the Apricot (*Prunus armeniaca* L.) [18]. During an outbreak, spongy moth can consume the entire foliage of trees and shrubs, as well as the herbs in the understory [19]. Spongy moth caterpillars have also been observed to eat the larvae of certain gall-maker wasps, such as *Biorhiza pallida* L. [20].

Spongy moth does not harm Thujas (*Thuja* spp.), Horse chestnut (*Aesculus hippocastanum* L.), or Buckthorns (*Rhamnus* spp.). It avoids species with high essential oil and poison

contents [16]. The caterpillars dislike Rhododendrons (*Rhododendron* spp.), Honey locust (*Gleditsia triacanthos* L.), Osage orange (*Maclura pomifera* C. K. Schneid), Catalpa (*Catalpa* spp.), American tulip tree (*Liriodendron tulipifera* L.), American coffee berry (*Gymnocladus dioicus* L.), and the Red mulberry (*Morus rubra* L.) [21]. Spongy moths do not consume Ash species (*Fraxinus* spp.) either [6,16]. However, according to the most recent publication, stress-induced food shortages can force spongy moth larvae to feed on the leaves of the European ash (*Fraxinus excelsior* L.) [22].

1.2. Host Plant Quality Determinants in the Feeding Ecology of the Spongy Moth

Studies have demonstrated a connection between the tree species preferred by the spongy moth and the nitrogen and protein contents of these trees. Hybrid Poplar species with a higher nitrogen content proved to be the best host for the larvae, enabling their optimal development [23]. In another experiment, Turkey oak (*Quercus cerris* L.), which has the highest soluble protein content and lowest C/N ratio, provided better conditions for larval development than the Sessile oak (*Quercus petraea* Liebl.) or Hungarian oak (*Quercus frainetto* Ten) [24]. The age of the leaves has a significant effect on herbivorous insects. Older leaves have lower water content and higher polyphenol and tannin contents, making them less favorable for insects [25]. This is confirmed by the observation of special seasonality in herbivore insects living in Hungarian oak stands, in which the highest number of species is found on fresh oak leaves at the beginning of the vegetation period [14]. Trees can be grouped based on when they produce new leaves. Quercus-type trees (e.g., *Quercus robur* and *Prunus padus*) grow mainly in the spring, while Populus-type trees (e.g., *Populus*, *Betula*, and *Alnus*) also produce foliage during the summer. As a result, larval development in herbivorous insects typically occurs in spring [26].

A plant uses various defense mechanisms to protect itself from herbivory. In this process, the plant faces a dilemma: how much of its resources should be used for protection or for growth to remain competitive among other plants [27]? Plants use both mechanical and chemical methods to protect themselves. Chemical protectants can either be produced consistently, as part of basic metabolism (constitutive), or as a reaction to herbivory [28,29]. Leaf consumption increases the phenol and hydrolyzed tannin contents, as well as the protein-binding ability of cells. These substances have a negative effect on the larval development of spongy moth. Therefore, plant responses can influence larval feeding behavior and affect population dynamics [30]. Turkey oak, for example, produces secondary metabolites in response to the spongy moth larvae's chewing. Phenols cause distorted larval development and high mortality rates in the population. Ellagic acid and a 0.5% increase in tannin concentration have the strongest effect on larvae [31]. The quality of the nutrients provided by the host plant is also influenced by the CO_2 concentration in the air [32].

1.3. Effects of Host Switching on Spongy Moth

In mixed forests, spongy moth larvae often encounter various tree species during their development and may switch hosts multiple times. Numerous field and laboratory studies have examined how feeding on different host plants in succession affects larval performance. Under favorable conditions, spongy moths generally adapt well to host switching, especially when the second host plant is also of high nutritional quality [33,34]. However, their development indices decline when they switch to an unfavorable host. Consequently, mixed forests, particularly those with a higher proportion of nutritionally poor host species, may reduce the risk of defoliation caused by spongy moths [35].

We examined how different host plant species influence the development of *L. dispar* by rearing caterpillars on either Turkey oak or Hornbeam. Additionally, we switched the hosts of two groups from Turkey oak to Hornbeam at various instars of larval development. All

investigations were carried out under laboratory conditions. In our experiment, we assessed three main aspects: (1) how different host plants, specifically Turkey oak and Common hornbeam, affect the larval development of spongy moth; (2) whether changing the host plant during larval development influences the speed, success, and other characteristics of development; and (3) how the timing of host plant rotation impacts larval development. With this laboratory experiment, we aimed to contribute to the broader understanding of how a polyphagous species develops in both monospecific (without host plant switching) and mixed-species (with potential host plant switching) forest stands. Although our findings are based on controlled conditions, they offer valuable insights into host-related developmental dynamics that may occur in natural forest ecosystems.

2. Materials and Methods

2.1. The Origin of the Samples

Eggs were collected for the laboratory experiment from Turkey oaks (*Quercus cerris* L.) and Common hornbeams (*Carpinus betulus* L.) in forest stands near Sopron, Hungary (compartments 17/A and 49/B, respectively), in March. Egg masses were kept in the refrigerator at 4–6 °C until the study began in April.

2.2. The Sample Groups

Four sample groups of spongy moths were reared under laboratory conditions. In two sample groups, we exchanged the host plants during the rearing experiment, whereas the other two groups were reared on the same (original) host only (see Table 1). Leaves for caterpillar rearing were collected from an individual Turkey oak and an individual European hornbeam. Each sample group contained 30 larvae chosen at the second larval instar.

Table 1. The main features of the dataset and their designations.

Sample Groups/Host Plants	Time of Changing Host Plant	Dataset Designations
Turkey oak [1]	–	Q
Turkey oak and Common Hornbeam	L_3 (L_4)	QC3
Turkey oak and Common Hornbeam	L_5	QC5
Common hornbeam [2]	–	C

[1] Turkey oak = *Quercus cerris*; [2] Common hornbeam = *Carpinus betulus*.

2.3. The Conditions of the Laboratory Experiment

The experiments were conducted in an insect-rearing chamber located in an air-conditioned room, with the temperature set to 20 °C and an 8 h dark/16 h light cycle. The caterpillars were fed leaves of the host plants, with the stems kept in Eppendorf tubes to preserve moisture.

2.4. The Course of the Experiment

Caterpillars hatching from egg masses were maintained together in one plastic box per host plant (Turkey oak or Common hornbeam). Individuals were chosen for the four sample groups in the second larval instar. We continued feeding three of the sample groups with Turkey oak and one with Hornbeam. At the third larval instar, we changed the host plant from Turkey oak to Hornbeam in one group. In another group (QC5), Turkey oak was exchanged for Hornbeam at the fifth larval instar. The caterpillars were kept in pairs as they progressed from the second to the fourth larval instar. After that, they were reared one by one until they pupated. Since individuals were assigned to the sample groups at L_2, the earliest opportunity for host switching was at L_3. The latest larval instar shared by both sexes is L_5, so this instar was used for the late host-switching treatment.

2.5. The Measured Data

During rearing, the weight of the caterpillars was measured daily from the fourth larval instar until pupation. The weight of the pupae was measured at pupation. The weight of the leaves belonging to the Turkey oak and Common hornbeam trees was measured in the following conditions:

- Wet weight: Measured before and after feeding (the leftovers).
- Dry weight: The leftovers were dried in a desiccator and weighed.
- Etalon weight: Each new portion of leaves was sampled, and both the wet and dry weights were recorded.

Furthermore, excrement was weighed at every larval stage. We also recorded the dates of egg hatching, larva molting, pupation, pupa hatching, and mating of the spongy moths.

2.6. The Calculated Data

The weight gain of the caterpillars was calculated at every larval instar with the following method:

$$\text{Weight gain (g)} = \text{the maximum weight of the individual (g)} - \text{the weight of the individual on the first day (g)}$$

We measured leaf consumption by weighing each leaf before and after exposure to the caterpillars. The remaining leaves were dried in an oven until they were completely dry, after which we measured the dry mass. To estimate the dry mass of the whole leaf, we dried and measured standard leaves. The dry weight of the consumed leaves, that is, dried leaf mass consumption, was calculated by subtracting the dry mass of the remaining leaves from the dry mass of the whole leaves.

We used nutritional indices such as the AD (approximate digestibility of leaf material in %), ECI (efficiency of converting ingested food into biomass in %), and ECD (efficiency of converting digested food into biomass in %), following the classical Waldbauer indices [36]. When calculating the indices, we used the fresh (i.e., not oven-dried) values of leaf mass consumption and frass mass. Regarding larval weight gain, no oven-dried mass data were available. The indices were calculated as follows:

$$\text{AD} = 100 \times (\text{leaf mass consumption (g)} - \text{weight of excrement (g)})/\text{weight of excrement (g)},$$

$$\text{ECI} = 100 \times \text{growth of larval weight (g)}/\text{weight of excrement (g)},$$

$$\text{ECD} = 100 \times \text{growth of larval weight (g)}/(\text{leaf mass consumption (g)} - \text{weight of excrement (g)}).$$

2.7. The Method of Analyses

The analysis was conducted using Microsoft Excel 365 and TIBCO Statistica 14 software. We applied basic statistical methods, including calculating the average, standard deviation, and maximum and minimum values.

Differences in developmental indicators among the four sample groups were examined using the non-parametric Kruskal–Wallis test. The assumptions required for conducting an ANOVA were not fully met: although the normality assumption was satisfied, homogeneity of variance was violated according to Levene's test. Considering the heterogeneity of variance and the limited sample sizes, the Kruskal–Wallis test was considered the most appropriate method for data analysis, since it is based on medians rather than means. Following the Kruskal–Wallis test, post hoc pairwise multiple comparisons of mean ranks between groups were performed.

3. Results

We observed substantial mortality in sample group C, where only 14 individuals reached the second larval instar (L_2) and could be selected. From the second larval instar onwards, sample group Q exhibited the lowest mortality rates among the groups studied (see Figure 1). In contrast, the highest number of dead individuals was found in sample group QC3 during this period. Although group C showed high sensitivity up to L_2, the mortality rate among the larvae that reached L_2 was relatively low. However, the mortality rate in this sample group was also the highest during the pupal stage. In the following analyses, we focus exclusively on the individuals that later transformed into adult butterflies.

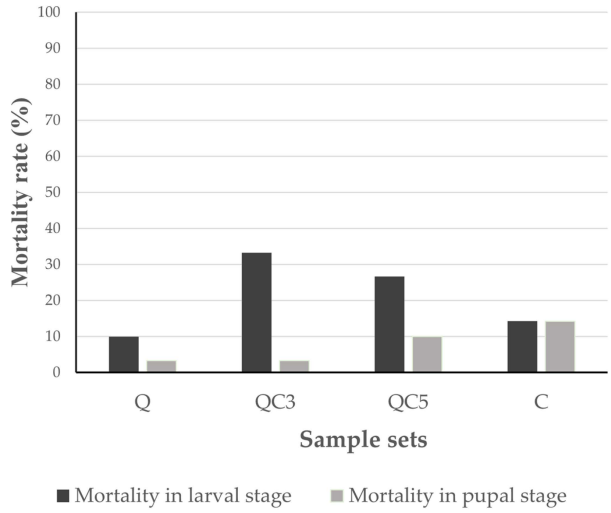

Figure 1. Mortality rate in larval (L_2–L_7) and pupal stages. Abbreviations: Q—fed with *Quercus*; QC3—fed with *Quercus*, switched to *Carpinus* at L_3; QC5—fed with *Quercus*, switched to *Carpinus* at L_5; C—fed with *Carpinus*.

Examining the development of the caterpillars, the spongy moths from sample group Q exhibited the shortest development time, while the development time of those from sample group C was the longest (see Table 2). The Kruskal–Wallis test indicated that this difference between groups Q and C was statistically significant. This trend was observed for both sexes during the larval stage and throughout the entire developmental period. The caterpillars that switched host plants had a development time between the values of the sample groups Q and C. The average development time for males in the QC3 sample group was slightly slower than that of males in the QC5 group. Group Q exhibited the longest pupal development period, with a significant difference compared to sample groups QC3 and QC5 among females.

Larval weight gain from the fourth larval instar is recorded in Table 3. The larvae from sample group Q exhibited the highest average weight gain during development. In contrast, the smallest increase in weight was observed in sample group C among males and in sample group QC3 among females. Notably, the weight gain of the females in sample group Q was significantly different from that of the other groups. In sample group QC5, some individuals of both sexes required an additional larval instar.

We observed variations in pupal weight among the different sample groups (see Table 4). Sample group Q had the highest pupal weight, while sample group C had the lowest. The pupal weights of spongy moths from groups QC3 and QC5 were intermediate, falling between the weights of groups Q and C. The differences in pupal weight between sample group Q and the other groups were statistically significant, except for the comparison between males in sample groups Q and QC3.

Table 2. Duration of development of spongy moths reared on different host plants.

Sample Sets [4]	Term of Larval Development (Days)					Term of Pupal Development (Days)				
	N	Average	Min [1]	Max [1]	SD [2]	*N*	Average	Min [1]	Max [1]	SD [2]
Males										
Q	15	44	37	53	4.6884	15	17	15	20	1.3452
QC3	5	46	44	50	2.3022	5	16	14	19	1.9494
QC5	11	49	44	54	3.8542	11	16	12	17	1.5667
C	7	52	49	55	2.2678	7	15	14	17	0.9759
Significant differences [3]:	L_1–L_3: Q–C, QC3–C; L_5: Q–QC3; entire larval development time: Q–C; entire development time: Q–C.									
Females										
Q	11	50	42	56	4.1187	11	15	13	16	0.9244
QC3	16	54	46	63	5.0658	16	13	11	16	1.6533
QC5	10	54	42	68	7.0087	10	13	11	15	1.0541
C	3	63	58	67	4.5092	3	14	13	14	0.5774
Significant differences [3]:	L_1–L_4: Q–C; entire larval development time: Q–C; development time of pupa: Q–QC3, Q–QC5; entire development time: Q–C.									

[1] end values; [2] standard deviation; [3] based on Kruskal–Wallis test ($p \leq 0.05$) and post hoc pairwise comparisons of mean ranks. Detailed results are provided in Supplementary Material Table S1. [4] Q—fed with *Quercus*; QC3—fed with *Quercus*, switched to *Carpinus* at L_3; QC5—fed with *Quercus*, switched to *Carpinus* at L_5; C—fed with *Carpinus*.

Table 3. The weight gain of caterpillars from L_4 to L_7 larval instars.

Sample Set [4]	L_4		L_5		L_6		L_7	Entire Larval Development [2]				
	N	Average	*N*	Average	*N*	Average		*N*	Average	Min	Max	SD
Males												
Q	15	0.1311	15	0.3274				15	0.4585	0.3752	0.5943	0.0641
QC3	5	0.1288	5	0.3063				5	0.4351	0.3522	0.5402	0.0747
QC5	11	0.1016	10 1	0.2945 0.1105	1	0.2407		11	0.3912	0.1616	0.6914	0.1556
C	7	0.0819	7	0.2945				7	0.3764	0.2913	0.4899	0.0825
Significant differences [3]:								-				
Females												
Q			11	0.3576	11	1.0752		11	1.4328	1.0008	1.8945	0.2931
QC3			16	0.2170	16	0.6174		16	0.8344	0.5149	1.3667	0.2406
QC5			10	0.2759	9 1	0.5428 0.3289	0.5022	10	0.8767	0.6497	1.4866	0.2368
C			3	0.1267	3 [1]	0.4462		3	0.8598	0.5803	1.0604	0.2496
Significant differences [3]:				L_5: Q–QC3, Q–C; L_6: Q–QC3, Q–QC5, Q–C; Entirely growth of larva weight: Q–QC3, Q–QC5.								

[1] two L_7 caterpillars were in the group. [2] larvae pupated at different instars were treated together. [3] based on the Kruskal–Wallis test ($p \leq 0.05$) and the post hoc pairwise comparisons of mean ranks. Detailed results are provided in Supplementary Material Table S1. [4] Q—fed with *Quercus*; QC3—fed with *Quercus*, switched to *Carpinus* at L_3; QC5—fed with *Quercus*, switched to *Carpinus* at L_5; C—fed with *Carpinus*.

The dry weight of leaves consumed by the larvae was calculated (see Table 5). Notably, this value was the lowest in sample group Q, despite these caterpillars achieving the greatest increase in larval weight. This suggests that the spongy moth larvae are more efficient at utilizing the nutrients from the Turkey oak. We attempted to clarify this relationship using nutrition indices (see Figure 2).

Table 4. Weight of spongy moth pupae reared on different host plants.

Sample Set [2]	*N* (db)	Average Pupal Weight	End Value of Pupal Weight (g)		SD of Pupal Weight
		g	min	max	g
Males					
Q	15	0.4274	0.3321	0.5490	0.0604
QC3	5	0.3655	0.3152	0.4266	0.0458
QC5	11	0.3180	0.2084	0.4322	0.0610
C	7	0.3017	0.2680	0.3356	0.0301
Significant differences [1]:		Pupal weight: Q–QC3, Q–QC5, Q–C			
Females					
Q	11	1.2027	0.8423	1.9082	0.3251
QC3	16	0.6126	0.3133	0.8287	0.1300
QC5	10	0.6318	0.5228	0.7866	0.0959
C	3	0.5273	0.4500	0.5729	0.0673
Significant differences [1]:		Pupal weight: Q–QC5, Q–C			

[1] based on the Kruskal–Wallis test ($p \leq 0.05$) and the post hoc pairwise comparisons of mean ranks. Detailed results are provided in Supplementary Material Table S1. [2] Q—fed with *Quercus*; QC3—fed with *Quercus*, switched to *Carpinus* at L_3; QC5—fed with *Quercus*, switched to *Carpinus* at L_5; C—fed with *Carpinus*.

Table 5. The dry weight of leaves consumed by spongy moths reared on different host plants.

Sample Set [4]	L_4		L_5		L_6		L_7	Entire Larval Development [2]				
	N	Average	*N*	Average	*N*	Average	Average	*N*	Average	Min	Max	SD
Males												
Q	15	0.1667	15	0.5647				15	0.7315	0.5337	1.0064	0.1358
QC3	5	0.2539	5	0.9336				5	1.1876	0.8795	1.7101	0.3349
QC5	11	0.1656	10 1	0.8618 0.2148	1	0.8822		11	1.1075	0.7242	1.8524	0.3182
C	7	0.1678	7	0.7725				7	0.9403	0.67	1.2704	0.2025
Significant differences [3]:			L5: Q–QC3; Q–QC5; Entire leaf weight consumed: Q–QC3; Q–QC5.									
Females												
Q			11	0.3278	11	1.8027		11	2.1305	1.0126	2.8683	0.6951
QC3			16	0.4572	16	1.957		16	2.4142	1.625	3.3224	0.4841
QC5			10	0.4739	9 1	1.7126 0.8125	1.9271	10	2.298	1.7024	2.9694	0.4336
C			3	0.2297	3 [1]	1.1416		3	2.6021	2.002	3.4533	0.7576
Significant differences [3]:								-				

[1] two L_7 caterpillars were in group C; [2] larvae pupated at different larval instars were treated together; [3] based on the Kruskal–Wallis test ($p \leq 0.05$) and the post hoc pairwise comparisons of mean ranks. Detailed results are provided in Supplementary Material Table S1. [4] Q—fed with *Quercus*; QC3—fed with *Quercus*, switched to *Carpinus* at L_3; QC5—fed with *Quercus*, switched to *Carpinus* at L_5; C—fed with *Carpinus*.

We observed the highest approximate digestibility (AD) among males in the sample group Q, while sample group C had the lowest AD (see Figure 2). For females, the highest AD was observed in the group raised exclusively on Hornbeam (C). Sample group Q showed the highest values for both males and females when the formulas incorporated larval weight (ECI, ECD). The Kruskal–Wallis test indicated that the nutritional indices

differed significantly among the sample groups, although the multiple comparisons did not indicate statistically significant differences between all groups.

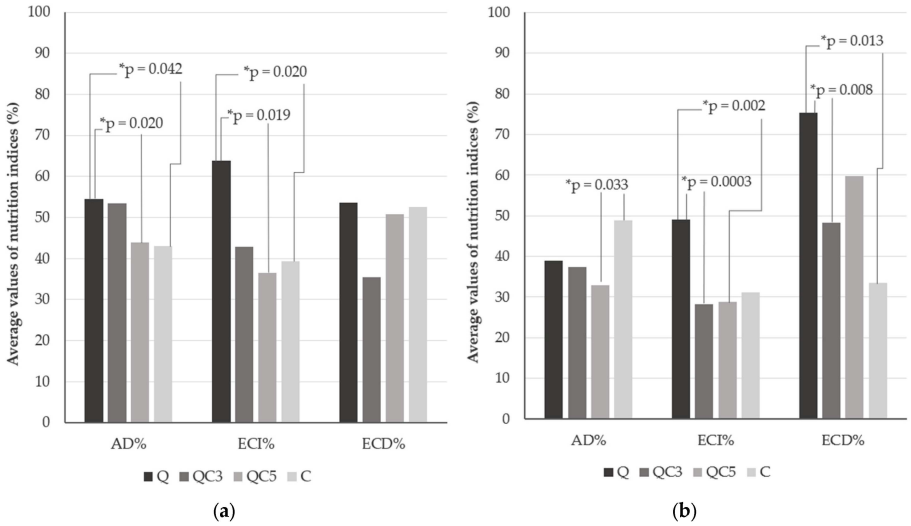

Figure 2. Average values of nutrition indices of male (**a**) and female (**b**) spongy moths reared on different host plants throughout the entire larval development period measured. * Significant differences between sample groups based on the multiple comparisons ($p \leq 0.05$) are indicated above the columns. Detailed results are provided in Supplementary Material Table S1. Abbreviations: Q—fed with *Quercus*; QC3—fed with *Quercus*, switched to *Carpinus* at L_3; QC5—fed with *Quercus*, switched to *Carpinus* at L_5; C—fed with *Carpinus*.

Our analyses revealed notable differences among the sample groups for several developmental variables, and these differences were not consistent between sexes. To summarize these patterns, we examined the proportion of developmental indicators showing statistically significant pairwise differences between sample groups based on post hoc comparisons following the Kruskal–Wallis test. This analysis synthesized previously identified statistically significant post hoc differences without additional testing. Most significant differences were observed between the Q sample group and the other groups, whereas the fewest differences occurred between QC3 and QC5 (see Figure 3).

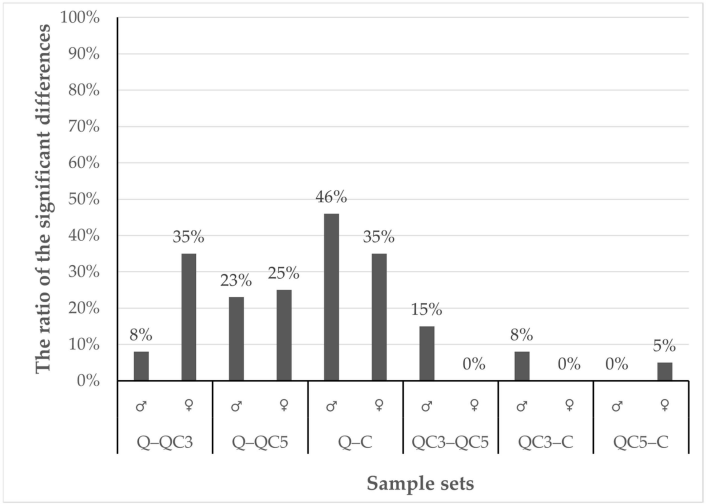

Figure 3. Ratio of significant differences regarding the examined development indices. The bars show the proportion of developmental variables with significant pairwise differences between sample groups, based on previously reported post hoc tests; no additional statistical testing was performed. Abbreviations: Q—fed with *Quercus*; QC3—fed with *Quercus*, switched to *Carpinus* at L_3; QC5—fed with *Quercus*, switched to *Carpinus* at L_5; C—fed with *Carpinus*.

4. Discussion

Our investigation aimed to explore how host switching influences the development of the spongy moth. To reduce the potential influence of less suitable host plant species on our results, we selected the primary host plants for the spongy moth based on Varga's research [6]. Specifically, we chose the Turkey oak and the Common hornbeam, both of which were found in the same location where we collected the spongy moth eggs.

Turkey oak was an appropriate choice for the experiment, given both its role as a preferred host for the spongy moth and its superior drought tolerance compared to other important European oaks [37,38]. This drought resistance could enhance the significance of Turkey oak, particularly in the context of climate change [34]. As European forests undergo significant transformations, the distribution range of many tree species is expected to shift, with the Turkey oak's range likely to expand [35]. These factors could make our results particularly relevant for forestry.

Significant differences were found in the mortality rate and several developmental indices of the sample groups. The group fed exclusively on Common hornbeam had the highest mortality. Only 14 specimens at L_2 were obtained, and several larvae and pupae were lost during further rearing. Therefore, the number of available individuals was insufficient to perform host switching in the opposite direction. This situation was confusing because the Common hornbeam is reported to be of the main host plants for the spongy moth [6]. However, some references do not classify certain Hornbeam species as primary host plants for the spongy moth. The American hornbeam (*Carpinus caroliniana* Walter) has been classified in the second category in terms of host plant suitability [39]. Mosher [12] reported that first-instar larvae died before or upon reaching the third instar in his study; we had a similar experience. Different Hornbeam species have varied in their suitability ranking. According to Miller et al. [40], the Common hornbeam was ranked as more suitable than the American hornbeam in a survey. At the same time, a more recent study compared the suitability of Turkey oak, European beech, and Common hornbeam for the feeding and development of spongy moth (*Lymantria dispar)* larvae. Among these three tree species, Hornbeam was clearly the least favorable host based on larval developmental and nutritional performance indices. This finding refines earlier observations and may partly explain the patterns observed in our own experiments [41].

The leaves used to feed the caterpillars were collected from a single Turkey oak and a single European hornbeam. These trees do not represent all individuals of their respective species, as leaf quality can vary both among different trees and within the same tree [20]. To minimize this variability, we purposely avoided using leaves from multiple individuals. Therefore, while our results are suitable for analyzing the effects of host switching, they are less appropriate for evaluating and comparing the suitability of different tree species as host plants for the spongy moth.

Host plant switching can occur between generations and even within the same generation. In the former case, if the spongy moth finds a suitable nutritional source, it can develop properly, regardless of the different nutritional sources used by its previous generations. This was confirmed by our earlier feeding experiments [42]. Under laboratory conditions, we successfully reared a spongy moth population from various hosts (*Populus* x *euamericana*, *Quercus ilex*, and *Quercus petraea*) and locations (Hungary, Croatia, and Austria) with a low mortality rate by feeding them exclusively on Pannónia poplar. These findings align with results from other laboratory experiments in which three different subspecies of *Lymantria dispar* (*L. dispar dispar*, *L. dispar asiatica*, and *L. dispar japonica*) of six provenances (Greek, American, Russian, Chinese, Korean, and Japanese) were reared on North American coniferous tree species. In this context, differences in development, vigor, and survival were primarily attributed to different nutritional sources. However, provenance was a crucial

factor influencing the spongy moth's growth, vigor, and survival when the same host plant was used. The differences between subspecies were less pronounced and significant in such cases [43]. In this study, we examined the effect of host alternation within a generation on the development of the spongy moth.

A shift to a less suitable host species adversely affects the developmental performance of *Lymantria dispar*, whereas switching to a more favorable host can exert a beneficial influence on larval development [35]. Moreover, evidence indicates that host quality, rather than the number of host species consumed or the specific timing of host switching, is the primary determinant of performance outcomes in this insect species [33]. Our findings partially support the conclusions drawn in previous studies.

On one hand, we observed elevated mortality in the host-switched groups (QC3, QC5) from the second instar to pupation, particularly in the group whose host changed during the third instar (L_3). These groups also exhibited poorer developmental indices compared with the larvae that fed exclusively on Turkey oak (Q), indicating that host switching can markedly influence developmental trajectories.

On the other hand, the pronounced performance differences among the sample groups may largely reflect that Turkey oak is a more suitable host than Common hornbeam under the conditions of our experiment. Consequently, the developmental performance of QC3 and QC5 generally exceeded that of the C group. This experience diverges from earlier observations in which larvae switched to a less suitable host exhibited reduced development compared with controls [35]. Notably, an additional larval stage was observed in two individuals from the QC5 sample group. Variation in the number of larval instars is a common phenomenon in insects, with supernumerary instars occurring more frequently under unfavorable developmental conditions [44]. Moreover, the quality of host plants has been shown to affect the number of larval instars in other foliage-feeding Lepidoptera [45].

We also investigated how the timing of host plant change influenced the outcomes based on the number of significant differences observed. The Kruskal–Wallis test revealed many significant differences between the Q sample group and the other groups (QC3, QC5, and C). However, fewer significant differences were observed between males in the QC3 and QC5 groups, and no differences were noted between females in the QC3 and QC5 groups. In conclusion, the development of the spongy moth is more significantly influenced by tree species and the occurrence of host plant changes than the timing of these changes.

One of our earlier studies [42] revealed significant differences in the development of male and female spongy moth larvae. In the current experiment, we observed that the two sexes reacted differently to changes in host plants. Female larvae demonstrated greater sensitivity to host alterations, as reflected in their weight gain and development time. In contrast, males exhibited more variability in the amount of leaf weight consumed. One possible explanation for the lower weight gain in female larvae is their flightlessness. Females may prefer a more permanent host due to their reduced ability to relocate. It has already been shown that females of the flightless subspecies (*Lymantria dispar dispar*) are more sensitive to their host plants, and they exhibit more active selection of plants compared to the flying subspecies (*Lymantria dispar asiatica* and *Lymantria dispar japonica*) [46].

There were notable differences in larval weight gain between the Q group and the host-switched groups. Female larvae in the QC3 group exhibited the lowest average weight gain. This reduced weight gain in female larvae may ultimately affect the number of viable eggs produced [47]. Consequently, it could lead to a decrease in the population size of the next generation. The compounds in host plants not only impact the larvae currently feeding on the plant but also influence their offspring. A lack of essential nutrients is negatively correlated with the number of eggs laid, which in turn reduces the cumulative nutrient content of the larvae [48]. Since these caterpillars have fewer nutrient reserves, they do not

tolerate starvation well, resulting in a lower survival rate. This phenomenon is known as the "maternal effect." Furthermore, the smaller weight gain observed in female larvae may suggest that flightless females prefer environmental constancy [49,50].

Our findings suggest that spongy moth larvae can develop on a lower leaf volume if they are feeding on suitable plants. This means that a preferred tree species could lose fewer leaves over the year. However, prior research [48] indicates that more suitable food conditions for spongy moths also have a favorable effect on reproductive capacity, which may lead to increased damage in subsequent years.

During outbreaks, when populations are sufficiently large, larvae can completely consume the foliage of their host tree. In such cases, the caterpillars may simply move on to another tree to continue feeding. In mixed forests, this behavior may force spongy moths to change their host plant, negatively affecting their growth. Consequently, feeding in a mixed stand is less advantageous for development than feeding in a homogenous stand. These factors contribute to a decline in population size, potentially resulting in reduced damage the following year.

5. Conclusions

Although the Turkey oak plays an important role in forestry, especially in the context of climate change, it is also essential to consider the benefits of mixed tree species. Our study indicates that the spongy moth, a dominant herbivorous species, thrives when feeding exclusively on Turkey oak. In a mixed forest, if the spongy moth switches to another tree species, such as European hornbeam, it may reduce damage caused by the next generation. Consequently, our study highlights the importance of biodiversity and the value of mixed forests.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f17030374/s1, Table S1: Significant differences between the sample groups.

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Abbreviations

The following abbreviations are used in this manuscript:

Q	The experimental group in which larvae were continuously fed with *Quercus* (Turkey oak) throughout their development.
C	The experimental group in which larvae were continuously fed with *Carpinus betulus* European hornbeam) throughout their development.
QC3	Larvae initially fed with *Quercus* and then switched to *Carpinus betulus* at the third instar.
QC5	Larvae initially fed with *Quercus* and then switched to *Carpinus betulus* at the fifth instar.
L_1–L_7	The larval instars (developmental stages) of *Lymantria dispar*.

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